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The anatomy of *Tudicla spirillus* (Linnaeus, 1767) and the relationships of the Tudiclidae (Gastropoda: Neogastropoda)

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ABSTRACT

Descriptions are provided for the morphology of the shell, operculum, radula, anatomy, egg capsules and juveniles of *Tudicla spirillus* (Linnaeus, 1767), the type species of the type genus of Tudiclidae. On the basis of these data, the family Tudiclidae is transferred from the Turbinelloidea to the superfamily Buccinoidea. Whether it maintains the rank of family or becomes subordinated among the subfamilies of Buccinidae will be determined by a thorough revision of the Buccinoidea and its families. Such a revision will likely expand Tudiclidae to include additional living genera, among them *Afer*, *Euthria*, and *Euthriostoma*.

Additional Keywords: Turbinelloidea, Buccinoidea, neogastropod phylogeny, anatomy, radula, radular morphology

INTRODUCTION

The family Tudiclidae, a widespread, diverse, and conspicuous component of tropical, shallow water, marine communities during the Late Cretaceous and Paleogene, has declined subsequently both in diversity and in geographical range. In the Recent fauna, it is believed to be represented by a single species, *Tudicla spirillus* (Linnaeus, 1767), restricted to the sublittoral sandy bottoms off southeastern India and Sri Lanka. As neither the anatomy nor the radular morphology of this, the type species of *Tudicla* were known, the composition and systematic relationships of the Tudiclidae had been inferred exclusively on the basis of shell morphology. Due to its distinctive shell features, there has been general agreement regarding the genera included in the family (e.g., Cossman, 1901, Dzhalilov, 1977; Saul, 1988). However, the taxonomic rank and phylogenetic relationships of the Tudiclidae have been subject to conflicting interpretations.

Cossman (1901: 60) proposed Tudiclinae [as Tudiculinae, based upon an unjustified emendation of *Tudicla* Röding, 1798] as one of four subfamilies of Turbinellidae, together with Turbinellinae, Fulgurinae, and Melongeninae. Because of their conchological similarity, Thiele (1929: 342) listed *Tudicula* H. and A. Adams, 1863, and *Afer* Conrad, 1858 as sections of *Tudicla*, and included this genus in the family Vasidae based on the radular morphology of *Tudicula*. Thiele (1929: 320) also reduced Melongeninae and Fulgurinae to genera and transferred them to the family Galeodidae [=Melongenidae]. Without referring to Thiele's work, Finlay and Marwick (1937: 69) elevated each of Cossman's turbinellid subfamilies to family rank, noting that "each marks and important group that has a separate history over a very long period, and each comprises a rich variety of form." Wenz (1943: 1303) followed Thiele (1929) in considering *Tudicula* to be among the subgenera of *Tudicla*, but regarded *Afer* to be a separate genus within the family Turbinellidae [as Vasidae]. Although some subsequent workers, primarily paleontologists, accord family status to this group (e.g., Zinsmeister, 1983; Saul, 1988; Stillwell and Zinsmeister, 1992), Tudiclidae had been regarded as a subfamily of the Turbinellidae by most contemporary workers (e.g., Rosenberg and Petit, 1987; Ponder and Warén, 1988; Harasewych, 1998, Bouchet et al., 2005, 2017). However, there has been little consensus as to the composition or taxonomic affinities of the Turbinellidae (= Xancidae = Vasidae). This family has been referred to the Buccinoidea (Sohl, 1964), the Volutoidea (e.g., Thiele, 1929; Wenz, 1943; Abbott, 1959; Taylor and Sohl, 1962) and the Muricoidea, both in the narrow (e.g., Stoliczka, 1867; Saul, 1988) and broad sense (e.g., Ponder, 1973; Boss, 1982; Ponder and Warén, 1988; Vaught, 1989; Stillwell et al., 2004; Bouchet et al., 2005), and most recently to the newly elevated superfamily Turbinelloidea (Fedosov et al., 2017; Bouchet et al. 2017).

The similarity between the names *Tudicla* Röding, 1798 and *Tudicula* H. and A. Adams, 1863 has caused numerous nomenclatural errors and confusion (reviewed by Rosenberg and Petit, 1987: 58; Saul, 1988: 881), which have obscured the evolutionary relationships between these conchologically similar but unrelated genera. The establishment of *Tudivasum* Rosenberg and Petit, 1987, as a replacement name for *Tudicula* should eliminate subsequent confusion with *Tudicla*.

Although *Tudicla spirillus*, the type species of *Tudicla*, is locally common, its distribution is limited to southeastern India and Sri Lanka at depths of 10–20 meters. It has been reported to occur in the Lakshadweep Islands off SW India (Bijukumar et al., 2015) and off Tamil Nadu, India (Apte, 2004).

Through the kindness of Deepak Apte of the Bombay Natural History Society and Dr. S. Antony Fernando of Annamalai University, I was able to examine a series of preserved specimens of *Tudicla spirillus*, its egg cases and juveniles. This report presents descriptions of the gross anatomy and spawn of *Tudicla spirillus*. The position of Tudiclidae within Neogastropoda is revised on the basis of these data.

MATERIALS AND METHODS

Specimens of *Tudicla spirillus* were trawled by fishermen between Porto Novo and Puducherry India at depths of 13–15 m, on a bottom of fine sand and mud. The shells of several living animals were cracked, and the specimens placed in 10% seawater formalin prior to shipment. Upon arrival in Washington, the remaining portions of shell were removed, and the fixed animals transferred to 70% ethanol, in which they were stored until dissected. Voucher material is deposited in the National Museum of Natural History, Smithsonian Institution (USNM 894130).

Radulae of *Afer afer* (Gmelin, 1791)(USNM 894131) collected in 15–25 m in Baie de Hann, Senegal, and *Afer cummingii* (Reeve, 1844) (ANSP 307296) from off Anping, Taiwan were obtained from dried specimens.

Shell fragments, larval shells, and radulae were mounted on conductive tape, coated with carbon and gold, and examined using a Hitachi S-570 Scanning Electron Microscope.

SYSTEMATICS

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815

Family Tudiclidae Cossmann, 1901

Tudiculinae Cossmann, 1901: 60 [based on unjustified emendation of *Tudicla* Röding to *Tudicula* (Cossmann, 1901:68)]
Tudiclidae Finlay and Marwick, 1937: 69.

Remarks: Tudiclidae has been well characterized by Finlay and Marwick (1937), Zinsmeister (1983), Saul (1988), and more recently by Stillwell and Zinsmeister (1992). Diagnostic conchological features include a short to moderately elevated spire, broadly shouldered whorls that have tubercles or axial nodules on the angulations, a long, axial siphonal canal, and a characteristic siphonal fold that varies in distinctness among included genera. Dzhalilov (1977) included the genera *Tudicla*, *Pyropsis* Conrad, 1860, *Pseudoperissolax* Clark, 1918, *Perissolax* Gabb, 1861, *Napulus* Stephenson, 1941, *Medionapus* Stephenson, 1941, *Perissitys* Stewart, 1927, and *Hercorhyncus* Conrad, 1868 in the family, and provided a phylogenetic scheme of the relationships among these genera. Zinsmeister (1988) also included *Cophocara* Stewart, 1927, *Heteroterma* Gabb, 1869, and *Nekewis* Stewart, 1927, while Saul (1988) added *Tudiclana* Finlay and Marwick, 1937, and *Rapopsis* Saul, 1988, to the genera comprising Tudiclidae.

Genus *Tudicla* Röding, 1798

Tudicla Röding, 1798: 145 (Type species, *Tudicla carinata* Röding, 1798 = *Murex spirillus* Linnaeus, 1767, by subsequent designation of Angas, 1878: 611).
Pyrella Swainson, 1835: 21 (Type species, *Turbinella spirillus*, by monotypy).
Spirillus F. Schlüter, 1838: 21 (Type species, *Pyrula rostratus* Schlüter, 1838 = *Pyrula spirillus*, by monotypy).
Pyrenella Gray, 1857: 11 (Type species, *Murex spirilla*, by monotypy).
Tudicula Ryckholt, 1862: pl. 33. Unjustified emendation of *Tudicla* (see Rosenberg and Petit,1987: 59)
Tudicula Cossmann, 1901: 68,70. Unjustified emendation of *Tudicla* (see Rosenberg and Petit, 1987: 59)

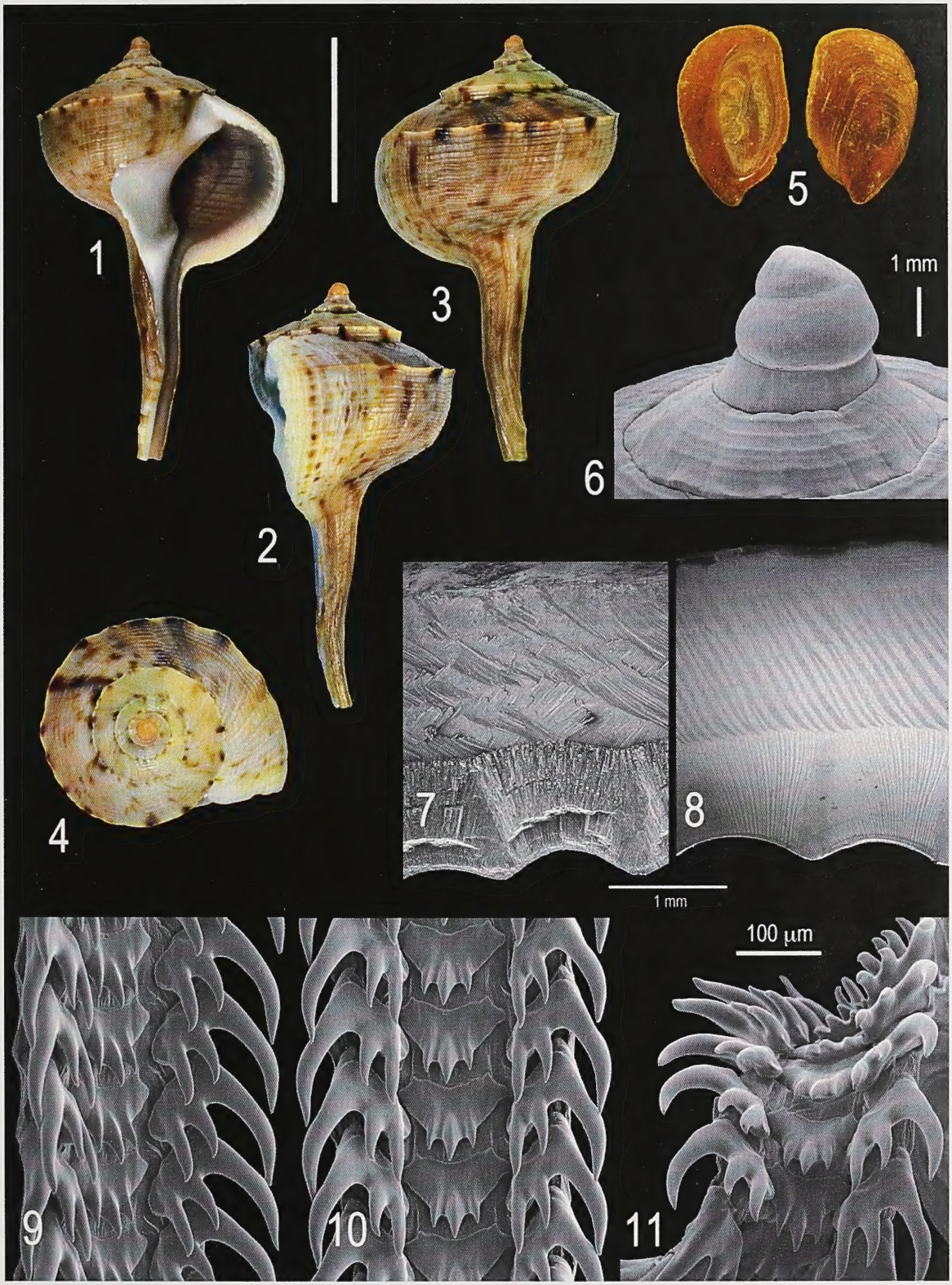
Remarks: The rounded body whorl, distinctive inductura, a long, well-demarcated siphonal canal, as well as a sharply defined siphonal fold distinguish *Tudicla* from related fossil genera.
Tudicla is reported to have ranged from eastern Africa (Cox, 1925) to Poland (Abdel-Gawad, 1986) during the uppermost Cretaceous. Paleogene occurrences span Europe and northern Africa, while Neogene records range from Europe to India and Australia. Abbott (1959: 31) reviewed the Recent species that had been referred to *Tudicla* by previous authors and concluded that only *T. spirillus* belongs to this genus. Rosenberg and Petit (1987:60) provide a list of nominal fossil species referable to *Tudicla*.

Tudicla spirillus (Linnaeus, 1767)

Figures 1–25, Table 1.

Murex spirillus Linnaeus, 1767: 1221, no. 554.
Tudicla carinata Röding 1798: 145.
Monoplex capitatus Perry, 1811: pl. 3, fig. 4.
Haustellum carinatum Schumacher, 1817: 213.
Spirillus rostratus Schlüter, 1838: 21.
Tudicla spirillus (Linnaeus).—H. and A. Adams, 1858:151.

Shell: Shell (Figures 1–4) medium-sized (to 85 mm), solid, with mammillated protoconch, low spire (spire angle 113°–122°), globose body whorl, and long, narrow, axial, siphonal canal. Protoconch (Figures 6, 16, 17) axial, cylindrical, increasing in diameter from 0.6 to 2.5 mm in 1¾ smooth, chalky whorls. Transition



Figures 1–11. *Tudicla spirillus* (Linnaues, 1767), USNM 894130, trawled between Porto Novo and Pondicherry, India, 13–15 m, fine sand and mud. **1.** Apertural, **2.** Lateral, **3.** Dorsal, and **4.** Apical views of the shell. **5.** Inner and outer surfaces of operculum. Scale bar = 3 cm for shell, 2 cm for operculum. **6.** Protoconch. **7–8.** Ultrastructure of adult shell. **7.** Fracture surface. **8.** Polished and etched surface. Collabral orientation, approximately 1 cm behind outer lip. **9–11.** Radula, in **9**. Oblique, **10.** Flat, and **11.** Folded orientation.

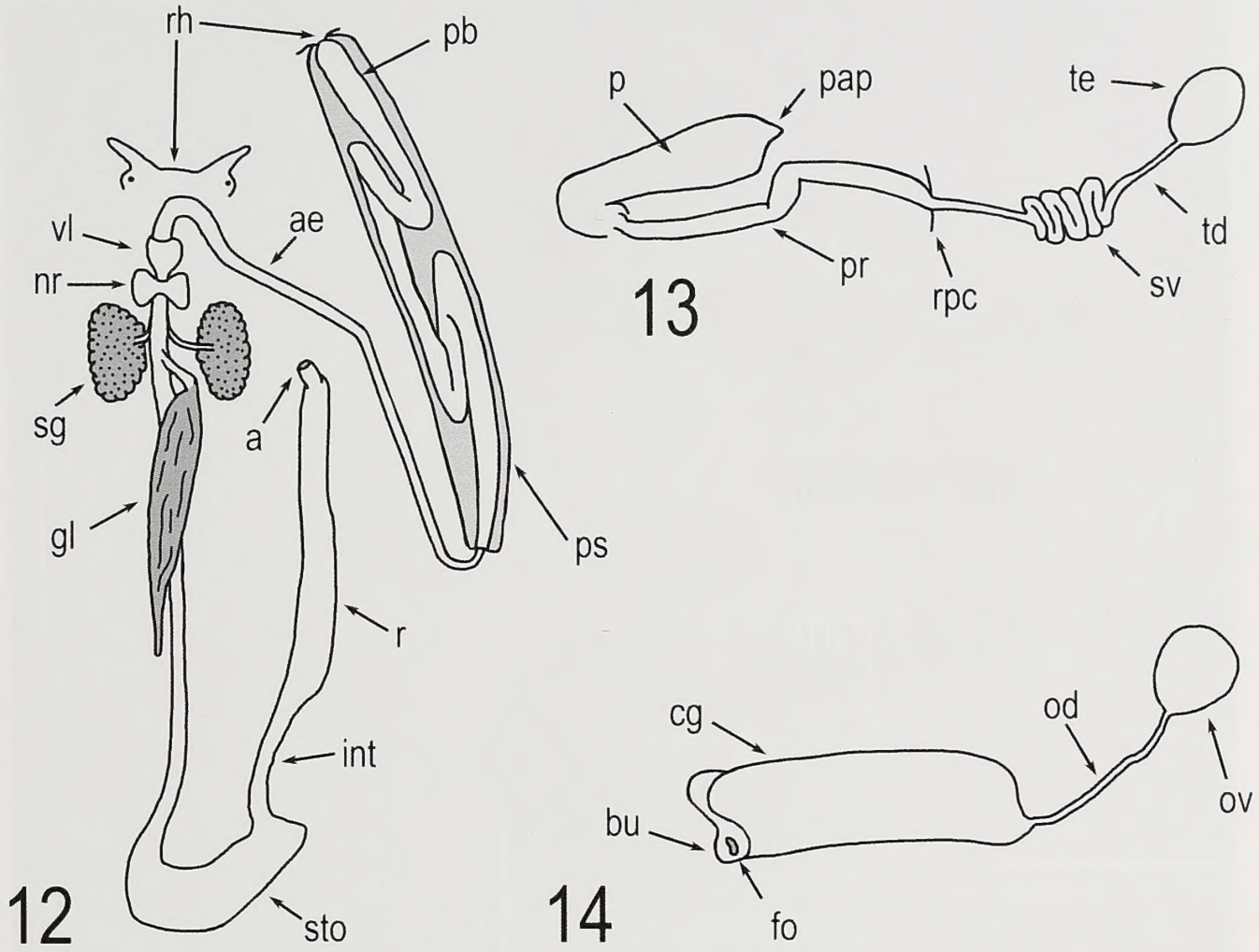
to teleoconch (Figures 16,17, arrows) demarcated by abrupt appearance of strong shoulder, axial and spiral sculpture. Teleoconch composed of up to 4½ convex, broadly shouldered whorls. Shoulder sharply keeled, with low, flat nodes along its periphery. Suture adpressed along first teleoconch whorl, flush with peripheral keel in subsequent whorls. In larger specimens (4+ teleoconch whorls), the suture may descend, abutting just below keel in last ¼–½ whorl, returning to near the keel at the thickened outer lip (Figure 2), possibly indicating determinate growth. Spiral sculpture of closely spaced cords, 13–17 between suture and shoulder, 21–28 between shoulder and siphonal canal, 7–13 along proximal ½ of siphonal canal. Axial sculpture limited to weak, flat nodes along the periphery (10–12 on body whorl) and weak growth lines or striae. Aperture elliptical, major axis deflected from shell axis of coiling by 32–35°. Outer lip thickened, with spiral lirae pronounced near lip but diminishing interiorly within ¼ whorl. As many as three sets of spiral lirae, spaced ½ to ¾ whorl apart, observed in sectioned shells. Spiral lirae number 5–8 between suture and shoulder, 16–22 between shoulder and siphonal canal. The inner lip is smooth, porcellaneous, with broad, flaring inductura along anterior half. Posterior canal delimited by pronounced callus at terminus of parietal ridge and most adaxial apertural lira. Columella with strong siphonal fold that continues onto inductura. Siphonal canal open, about ½ shell length, and weakly sinuate. Narrow inductural callus extends to siphonal fasciole situated near midpoint of siphonal canal. Protoconch pinkish tan. Teleoconch pinkish tan, mottled with reddish brown spots. Early whorls generally lightest in color, distal half of the siphonal canal darkest. Aperture and inductural callus white. Periostracum, where present, very thin, composed of very fine minutely hirsute lamellae, generally abraded away. Operculum (Figure 5) corneous, broadly unguiculate, with terminal nucleus, attachment area that spans most of inner surface, except for broad, glazed, free band along abaxial edge. The operculum fills the aperture within 1/6 whorl of the outer lip.

Ultrastructure: Outer lip of adult shells composed of two orthogonal layers of crossed-lamellar aragonite (Figures 7, 8). Outer layer, with crystal faces colabrally aligned, is thicker (~ 1.5 mm), comprises spiral and axial sculptural elements. Inner layer, with crystal faces perpendicular to growing edge, thickest (~ 1.0 mm) along the outer lip, and comprises apertural lirae, callus and inductura. Larval shells (ex-capsule) are composed a single layer (~ 50 μm thick) of collabrally oriented crystals (Figure 18).

External Anatomy: Retracted soft parts comprise 2¾ whorls. Pallial cavity spans ½ whorl, kidney ¼ whorl, digestive gland 1¾ whorls. Foot nearly as broad as long, operculum spanning entire foot width. Preserved animals pinkish tan, weakly mottled with small, dark brown dots, resembling shell in pattern and color. Siphon long and simple, with broad, muscular fold that spans inductura at its inner proximal inner edge. Head small, with short tentacles that barely extend beyond the small eyes.

Pallial Cavity: Pallial cavity shallow, broad, with organs disposed as in other neogastropods (Ponder, 1974: fig. 5). Mantle edge slightly thickened, with small papillae along its adapical half. Osphradium is 2/3 as wide, 7/8 as long as ctenidium. A narrow gap separates narrow hypobranchial gland from ctenidium. Hypobranchial gland composed of chevron-shaped pleats that line apex of the pallial cavity and extend only slightly onto rectum and pallial gonoducts. No purple pigment was detected in any of the specimens examined.

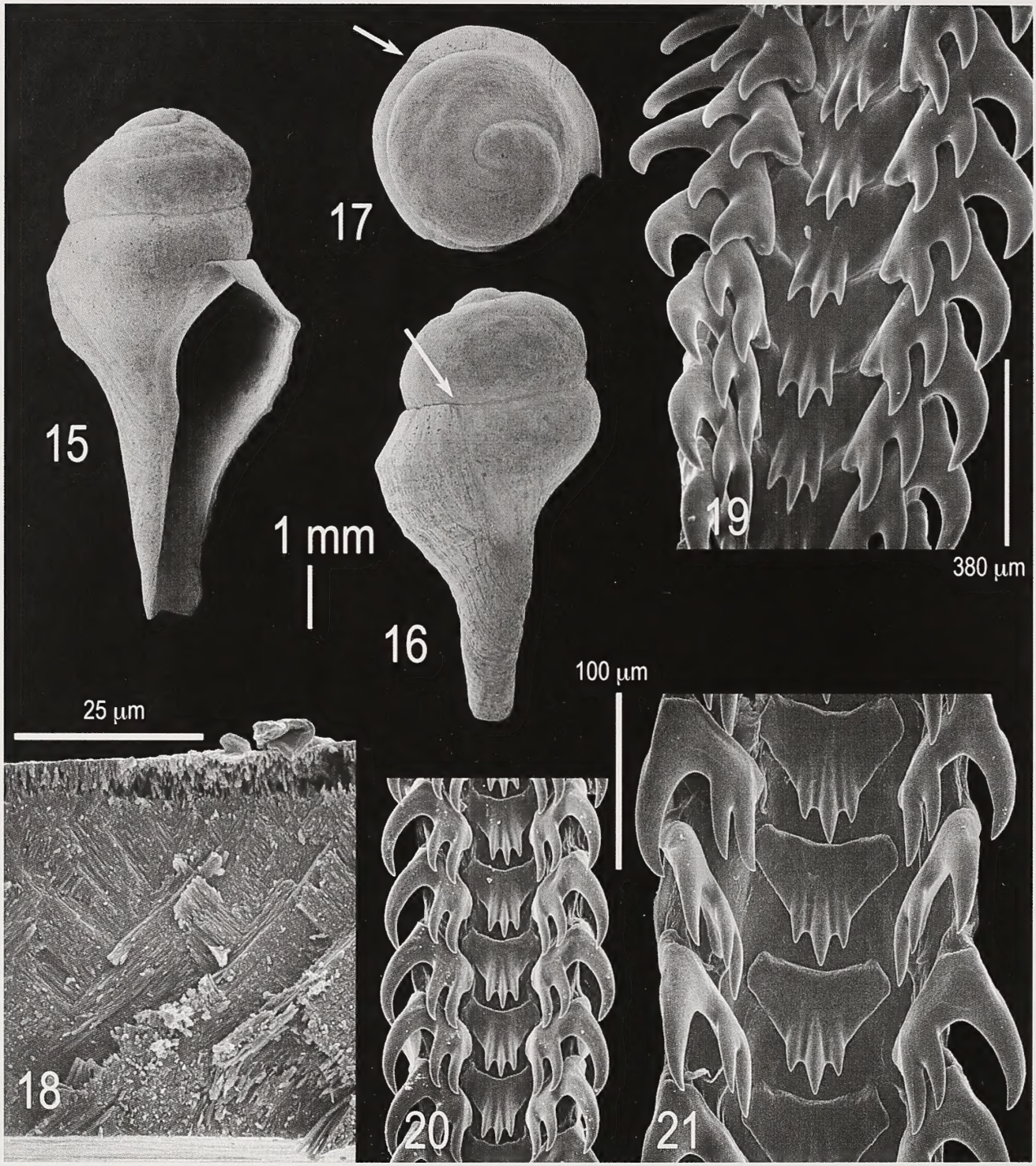
Alimentary System: Rhynchostome (Figure 12, **rh**) leads to long proboscis sheath (Figure 12, **ps**) that fills entire cephalic hemocoel. Numerous short muscle fibers attach it to dorsal and lateral walls of hemocoel, while a long retractor muscle extend from its midpoint to the rear of the hemocoel where it joins the columellar muscle. Proboscis sheath muscular anteriorly, thin posteriorly, containing convoluted, retracted proboscis (Figure 12, **pb**) that approximates the shell in length when extended. Buccal cavity nearly as large as the small (3 mm) buccal mass. Radular sac long (~ 11 mm), containing triserial radula of 116–122 (n = 5) rows of teeth, each row composed of a tricuspid rachidian tooth flanked on each side by a tricuspid lateral tooth (Figures 9–11). Rachidian teeth very slightly broader than lateral teeth, with 3 cusps emerging from the central third of a broadly attached basal plate. Outermost cusp of lateral teeth twice as long, thicker than central and inner cusps. The anterior esophagus (Figure 12, **ae**), which contains the ducts of the salivary glands embedded beneath the dorsal folds, runs through the proboscis, from the posterior end of the proboscis sheath along its ventral surface to the nerve ring at the anterior margin of the cephalic hemocoel. Salivary glands (Figure 12, **sg**) lie beneath the proboscis sheath near the nerve ring. Accessory salivary glands are absent. A slight swelling of the esophagus just anterior to the nerve ring marks the valve of Leiblein (Figure 12, **vl**). After passing through the nerve ring the mid-esophagus is joined by a narrow duct from the gland of Leiblein (Figure 12, **gl**). This gland is short, flaccid, brownish, transluscent, tapers posteriorly, and does not reach the rear of the hemocoel. The posterior esophagus runs along the floor of the hemocoel together with the anterior aorta and paired odontophore retractor muscles, and joins the stomach (Figure 12, **sto**) along the anterior face of the digestive gland. The tubular stomach forms a nearly complete circle along the anterior and dorsal surfaces of the digestive gland. A distinct caecum is present in the stomach and the ducts of the digestive gland are widely separated, lying at opposite ends of a gastric lumen bounded by large, irregular typhlosoles. The intestine (Figure 12, **int**) is narrow, broadens upon entering the mantle cavity to form the rectum (Figure 12, **r**), then again constricts, running alongside the pallial gonoduct and terminating roughly 1 cm from the mantle edge. The anus (Figure 12, **a**) is detached from the pallial wall and lacks a papilla. An anal gland is not present.



Figures 12–14. Anatomical features of *Tudicla spirillus*. **12.** Alimentary system. **13.** Male reproductive system. **14.** Female reproductive system. Abbreviations: **a,** anus; **ae,** anterior esophagus; **bu,** bursa copulatrix; **cg,** capsule gland; **gl,** gland of Leiblein; **int,** intestine; **nr,** nerve ring; **od,** oviduct; **ov,** ovary; **p,** penis; **pap,** papilla; **pb,** proboscis; **pr,** prostate; **ps,** proboscis sheath; **r,** rectum; **rh,** rhynchostome; **rpc,** rear of pallial cavity; **sg,** salivary gland; **sto,** stomach; **sv,** seminal vesicle; **td,** testicular duct; **te,** testis; **vl,** valve of Leiblein.

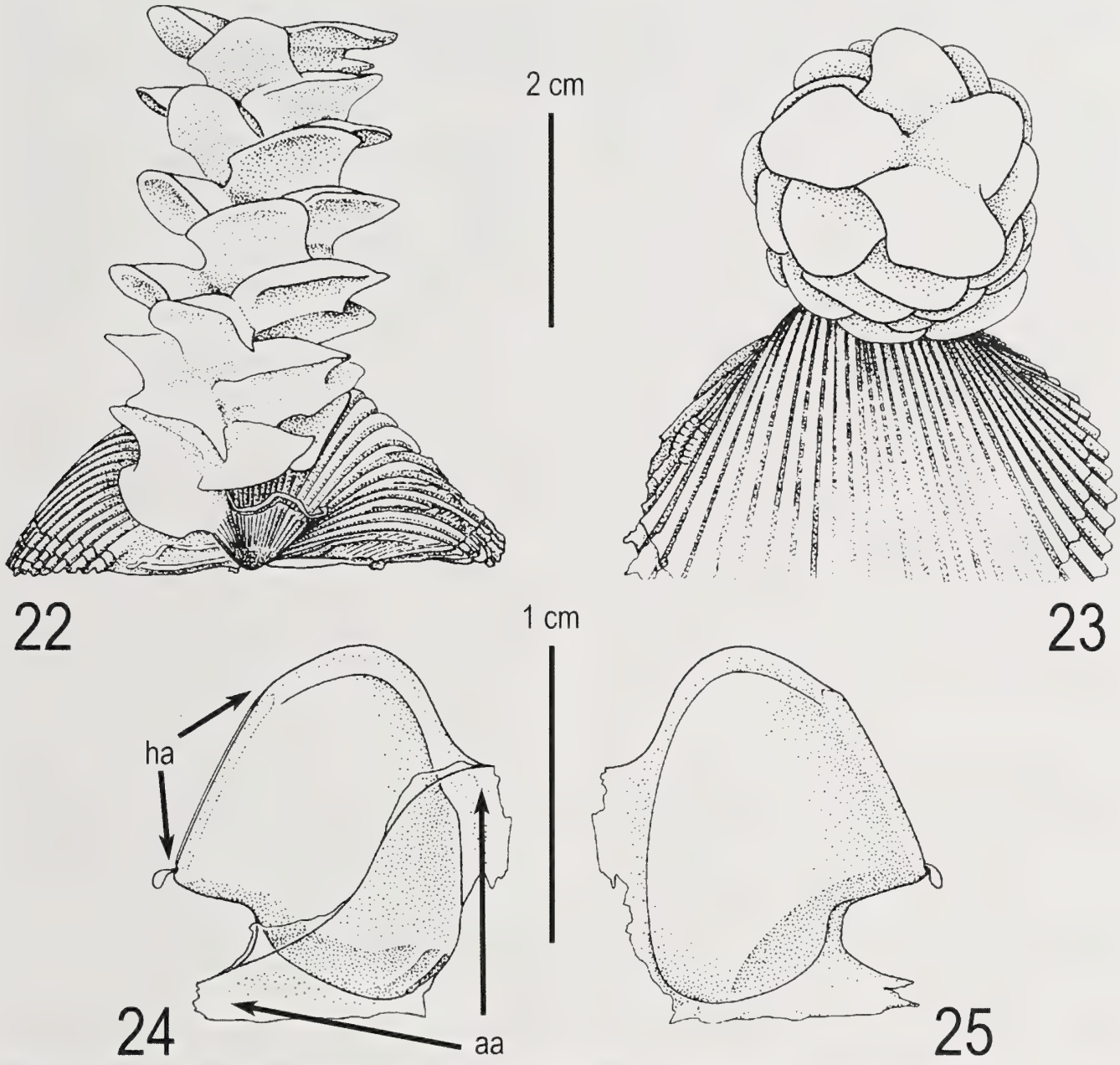
Male Reproductive System: The testis (Figure 13, **te**), lines the adapical and adaxial sides of the digestive gland. A testicular duct (Figure 13, **td**) runs anteriorly, forming a convoluted seminal vesicle (Figure 13, **sv**) that extends from the posterior portion of the stomach, along the kidney, across the posteriormost region of the pericardium, to the rear of the pallial cavity (Figure 13, **rpc**), where it expands to become thick, glandular, and surrounded by a thick muscle layer. The prostatic portion of the duct (Figure 13, pr) runs along the pallial wall, descends to the floor of the mantle cavity at mid-length and leads to the base of the penis (Figure 13, **p**). The penis is short (spanning < ½ the mantle cavity when retracted), dorsoventrally compressed, broadest near the distal end, and has a broadly conical papilla (Figure 13, **pap**). The duct is situated within the central portion of the penis.

Female Reproductive System: The ovary (Figure 14, **ov**) lines the adaxial side of the digestive gland and is composed of a series of acinous tubules that converge on the oviduct (Figure 14, **od**). This narrow, translucent duct leads anteriorly, joining the pallial gonoduct at the right anterior wall of the kidney. The pallial gonoduct is composed of a long (~ 25 mm), tubular (~ 9 mm diameter) capsule gland (Figure 14, **cg**) and a bursa copulatrix (Figure 14, **bc**). No morphologically distinct ingesting gland or albumen gland were discerned. The capsule gland has thick, glandular walls and a sigmoidal dorso-ventral lumen. The posterior ¼ of the gland differs in color and consistency, its lumen is continuous with that of the anterior portion of the gland but rotated about 30° counter-clockwise. At the anterior margin of the capsule gland, two darkly pigmented bands of tissue flank the lumen at the entrance of the duct from the bursa copulatrix. The bursa copulatrix (Figure 14, **bu**) consists of a coiled glandular tube enclosed in a mass of connective tissue. An adjacent anterior flap protects its opening (Figure 14, **fo**).



Figures 15–21. *Tudicla spirillus* (Linnaeus, 1767). **15.** Apertural, **16.** Dorsal, and **17.** Apical views of pre-emergent hatchlings. Arrow indicates transition between protoconch and teleoconch. **18.** Fracture surface of hatchling shell, collabral orientation, approximatly 1 mm behind outer lip. **19.** Radula of hatchling. **20.** Radula of *Afer afer* (Gmelin, 1791), USNM 894131, from 15–25 m, off Baie de Hann, Senegal. **21.** Radula of *Afer cummingii* (Reeve, 1844), ANSP 307296, from off Anping, Taiwan.

Spawn: The spawn mass of *Tudicla spirillus* (Figures 22–23) was briefly discussed and illustrated by Pinn (1992), who attributed it to this species by deduction. It is described in more detail here. It consists of a columnar, double helical arrangement of 40–56 (n = 8) capsules forming a left-handed spiral. Individual strands are anchored to hard substrates (shells, rocks) or branch from conspecific egg strands. Capsules are deposited as



Figures 22–25. *Tudicla spirillus* (Linnaeus, 1767). **22.** Lateral and **23.** Dorsal views of complete egg strand attached to a cardiid valve. **24.** Ventral and **25.** Dorsal views of individual egg capsule. Abbreviation: **ha,** preformed hatching aperture.

roughly opposing pairs, and attached along their bases at angles of 48–106° (counterclockwise) from the preceding pair, forming and offset, pentagonal arrangement (Figure 23). Individual capsules (Figures 24, 25) are roughly discoidal, strongly asymmetrical, with a broad attachment area and a wide, outwardly directed, pre-formed hatching aperture sealed with a mucoprotein plug. The number of ova initially deposited in each capsule is unknown. Ten capsules from each of eight strands were examined and each invariably contained two juveniles (Figures 15–17) ready to hatch.

Kidney: The large kidney (spanning ¼ whorl) is situated to the right of an elongated pericardium. The nephridial gland, which borders the entire length of the pericardium along the dorsal left surface of the kidney, is 3–4 times broader anteriorly than posteriorly. Viewed from within the kidney, this organ is composed of vertical fibrous bundles, separated by narrow, slit-like invaginations. The kidney is of the *pycnonéphridiens* type (Perrier, 1889) with the primary and secondary lamellae interdigitated along the dorsal and lateral walls of the kidney. The primary lamellae, emanating from the ventral branch of the afferent renal vein, number 7–8, and are heavily pleated. The secondary lamellae, emanate from the dorsal branch of the afferent renal vein, are weak in the anterior portion of the kidney, becoming more conspicuous posteriorly.

Table 1. *Tudicla spirillus*. Measurements of shell characters. Linear measurements in mm. (n = 10). Juveniles (n =10) all from a single strand of capsules.

Character	Mean	SD	Range
Adults			
Shell length (SL)	68.6	6.6	57.9–75.9
Shell width (SW)	39.4	3.7	33.0–45.1
Aperture length (AL)	22.1	2.1	19.5–25.7
Siphonal canal length (SCL)	35.5	3.9	28.9–40.8
AL/SL	0.323	0.016	0.290–0.342
SCL/SL	0.517	0.016	0.498–0.617
Spire Angle	117.1°	4.28°	113.8°–121.5°
Whorls, protoconch	1.75	0.12	1.5–2.0
Whorls, teleoconch	3.96	0.26	3.7–4.5
Nodes along shoulder	11.4	0.8	10–12
Spiral cords			
Suture – shoulder	14.1	1.1	13–17
Shoulder – siphonal canal	24.6	2.1	21–28
Siphonal canal	9.1	1.7	7–13
Juveniles at Hatching			
Shell length	7.1	0.5	6.5–8.3
Whorls, protoconch	1.8	0.3	1.5–2.7
Whorls, teleoconch	0.5	0.1	0.3–0.8

Nervous System: The nervous system is of the typical stenoglossan type, with all circum-esophageal ganglia highly concentrated. The supra-esophageal ganglion is closely attached to the right pleural ganglion.

DISCUSSION

The attribution of extinct genera to Tudiclidae by paleontologists has been based on distinctive shell features shared with the type species *Tudicla spirillus*, presumed to be the only living species within the family. Abbott (1959) recognized the relationship of living species of the genus *Tudicula* (now *Tudivasum*, see Rosenberg and Petit, 1987) to *Vasum* based on morphology of both shell and radula, but did not consider *Tudicla* to be closely related to either of these genera. As the anatomy and radular morphology of *Tudicla* had not been studied, the inclusion of Tudiclidae within Turbinelloidea has been tentative, based on similarities of its shell to those of some species of *Tudivasum*.

The anatomy of *Tudicla spirillus* conforms to the basic neogastropod ground plan (Ponder, 1974). Several features, among them the absence of accessory salivary glands, and a kidney of the *pycnonéphridiens* type are consistent with those characterizing the superfamily Buccinoidea and at least some members of the Turbinelloidea (Ponder, 1974: Table 2). Other features, such as the lack of columellar folds in the shell and the absence of an anal gland, are shared with Buccinoidea, but not with Turbinelloidea. Although Ponder (1974: Table 2) reported that an anal gland was present in Turbinellinae but absent in Vasinae, Medinskaya et al. (1996: 60) reported that it was present but very small in *Vasum muricatum*. The occurrence of a long proboscis folded within a proboscis sheath is prevalent in Turbinelloidea but also occurs in some buccinoideans (e.g., Melongenidae, Colubrariidae), while a sperm duct that is closed throughout the pallial cavity and passes through the central portion of the penis in *Tudicla spirillus*, differs from the open pallial sperm groove and penial groove that occur in Turbinelloidea.

The morphology of the egg mass of *Tudicla spirillus*, with the first several capsules attached to a hard substrate and subsequent capsules added with preformed hatching apertures directed outwardly in a columnar array, resemble those of the buccinid genus *Neptunea* Röding, 1798 (e.g., see Golikov, 1963: figs. 70, 72; pl. 26, fig. 1a). Egg capsules of *Turbinella pyrum* and *Turbinella angulata* resemble those of Busyconinae, comprising a linear strand in which each of 10–28 coin-shaped capsules is attached at its base, parallel to the previously deposited capsule. Earliest capsules are buried in the sand to form an anchor, subsequent capsules are free forming a strand (Hornell, 1951:24, fig. 20; Bandel, 1976: figs. 17a–c, 19). Spawn of *Vasum muricatum* contain from 3 (D'Asaro, 1970: figs. 7a–b) to 13 capsules (Bandel, 1976: figs. 16a–b, 19), Each capsule was broad and low, individually attached to the substratum, with the hatching aperture situated apically.

The morphology of the radula of *Tudicla spirillus*, particularly the presence of tricuspid rachidian teeth and tricuspid lateral teeth with the outer cusp longest, most clearly precludes the inclusion of Tudiclidae in Turbinelloidea and indicates a relationship within the Buccinoidea. Fraussen and Haddorn (2000) transferred the genus *Afer* from the Turbinellidae to Buccinidae based upon examination of the radulae of several species, which they reported as being typically buccinid, noting similarities to the radular teeth of *Buccinulum vittatum* (Quoy

and Gaimard, 1833) and *Euthria cornea* (Linnaeus, 1758). The radula of *Afer afer* (Gmelin, 1791) (Figure 20) the type species of *Afer*, and *Afer cummingii* (Reeve, 1844) (Figure 21) are extremely similar to those of *Tudicla spirillus*, suggesting a close relationship.

Based on these observations, the family Tudiclidae is transferred from the Turbinelloidea to the superfamily Buccinoidea. Whether it retains the rank of family, or becomes subordinated among the subfamilies of Buccinidae will require a thorough revision of the Buccinoidea and its constituent families and subfamilies. Such a revision will likely expand Tudiclidae to include additional living genera, among them *Afer*, *Euthria* and *Euthriostoma*.

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A new freshwater bivalve species of the genus *Cyclonaias* from Texas (Unionidae: Ambleminae: Quadrulini)

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ABSTRACT

Cyclonaias necki, a new species from the San Marcos River in the San Antonio/Guadalupe River Basin in Gonzalez County, Texas, USA, is here described and separated from *Cyclonaias petrina* based on shell morphology and molecular barcoding analyses.

Additional Keywords: Freshwater Bivalve, San Marcos River, Guadalupe County, Caldwell County

INTRODUCTION

On the last revision of the freshwater mussels of the United States of America and Canada, 14 *Cyclonaias* species were recognized (Williams et al., 2017), six of which occur in Texas (Howells, 2013). One of these species is the Texas Pimpleback *Cyclonaias petrina* (Gould, 1855) distributed across the Colorado and San Antonio/Guadalupe River systems. However, specimens recently collected for this study in the San Marcos River in the San Antonio/Guadalupe River Basin, revealed clear conchological and genetic differences from those in the Colorado basin, raising the question of the existence of two distinct species in south central Texas. This paper presents the description of *Cyclonaias necki* new species. **A subset of the authors of the current paper, Burlakova, Karatayev, Lopes-Lima, and Bogan, are the authors of the new species.**

MATERIALS AND METHODS

Eleven specimens, all previously identified as *Cyclonaias petrina*, were collected from the Concho River (Colorado River Basin) [4 specimens], San Saba River (Colorado River Basin) [3 specimens] and San Marcos River (San Antonio/Guadalupe River Basin) [5 specimens] (Table 1) in 2008–2011, as part of the project "State-wide Assessment of Unionid Diversity in Texas" (Federal Aid Grant No. T-43 funded by the US Fish and Wildlife Service State Wildlife Grant Program through the Texas Parks and Wildlife Department (TPWD), 2008–2012). The work was carried out with an appropriate Scientific Research

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Table 1. List of all individual specimens used for genetic analyses, catalog numbers, collection sites, and GenBank references. BSGLC (SUNY Buffalo State College Great Lakes Center); NCSM (North Carolina Museum of Natural Sciences); UF (Florida Museum of Natural History).

Species	Locality	Catalog number	River (Basin)	GenBank
Cyclonaias petrina	Paint Rock	BSGLC 1617	Concho River (Colorado)	MG969416
Cyclonaias petrina	Paint Rock	BSGLC 1619	Concho River (Colorado)	MG969417
Cyclonaias petrina	Paint Rock	BSGLC 1620	Concho River (Colorado)	MG969418
Cyclonaias petrina	San Saba	BSGLC 3254	San Saba River (Colorado)	MG969419
Cyclonaias petrina	San Saba	BSGLC 3255	San Saba River (Colorado)	MG969420
Cyclonaias petrina	San Saba	BSGLC 2157	San Saba River (Colorado)	MG969421
Cyclonaias necki	Palmetto State Park	BSGLC 1672	San Marcos River (San Antonio/Guadalupe)	MG969422
Cyclonaias necki	Luling	NCSM 65378	San Marcos River (San Antonio/Guadalupe)	MG969423
Cyclonaias necki	Luling	BSGLC 2255	San Marcos River (San Antonio/Guadalupe)	MG969424
Cyclonaias necki	Luling	BSGLC 2256	San Marcos River (San Antonio/Guadalupe)	MG969425
Cyclonaias necki	Luling	UF 441084	San Marcos River (San Antonio/Guadalupe)	KT285656

Permit SPR-0503-300 issued by the TPWD. Specimens were placed in 99% ethanol for molecular analyses. The holotype and a paratype were deposited in the North Carolina Museum of Natural Sciences (NCSM), and the remaining paratypes and other specimens in the Great Lakes Center Invertebrate Collection (BSGLC) (SUNY Buffalo State College, Buffalo, NY) (Tables 1, 2).

Sequencing, PCR Amplification, and Dataset Construction: For each sample, amplification and (bidirectional) sequencing was carried out for cytochrome c oxidase subunit I (COI) with the primers LCO_22me and HCO_700dy (Walker et al., 2006) with annealing temperature of 50°C and the remaining polymerase chain reaction (PCR) conditions as described in Froufe et al. (2014). Sequences were obtained with the BigDye sequencing protocol (Applied Biosystems 3730xl) by Macrogen Inc., Korea. Forward and reverse sequences were edited and assembled using ChromasPro 1.7.4 (Technelysium, Tewantin, Australia). All new sequences have been deposited in GenBank (Table 1). A COI dataset was then constructed with the newly sequenced individuals and one *Quadrula petrina* present in GenBank (Table 1) [San Marcos River, southwest of Luling, Caldwell/Guadlupe County Line, Texas (Pfeiffer et al., 2016)]. The dataset was aligned using the MAFFT multiple sequence alignment algorithm (Katoh and Standley, 2013) with default parameters.

Molecular-based Species Delineation Methods: Two distinct molecular methods were applied to determine the number of Molecular Operational Taxonomic Units (MOTUs). The first is distance based, i.e. the BIN system implemented in BOLD (Ratnasingham and Hebert, 2013) widely used as the standard COI barcoding method. For the BINs system, the COI dataset was analyzed with the Cluster Sequences tool implemented in BOLD 4 (http://v4.boldsystems.org) (Ratnasingham and Hebert, 2013). The second species delineation method used the 95% statistical parsimony connection limit in TCS 1.21 (Clement et al., 2000).

SYSTEMATICS

Class Bivalvia Linnaeus, 1758
Order Unionida Gray, 1854
Family Unionidae Rafinesque, 1820

Genus *Cyclonaias* Pilsbry in Ortmann and Walker, 1922

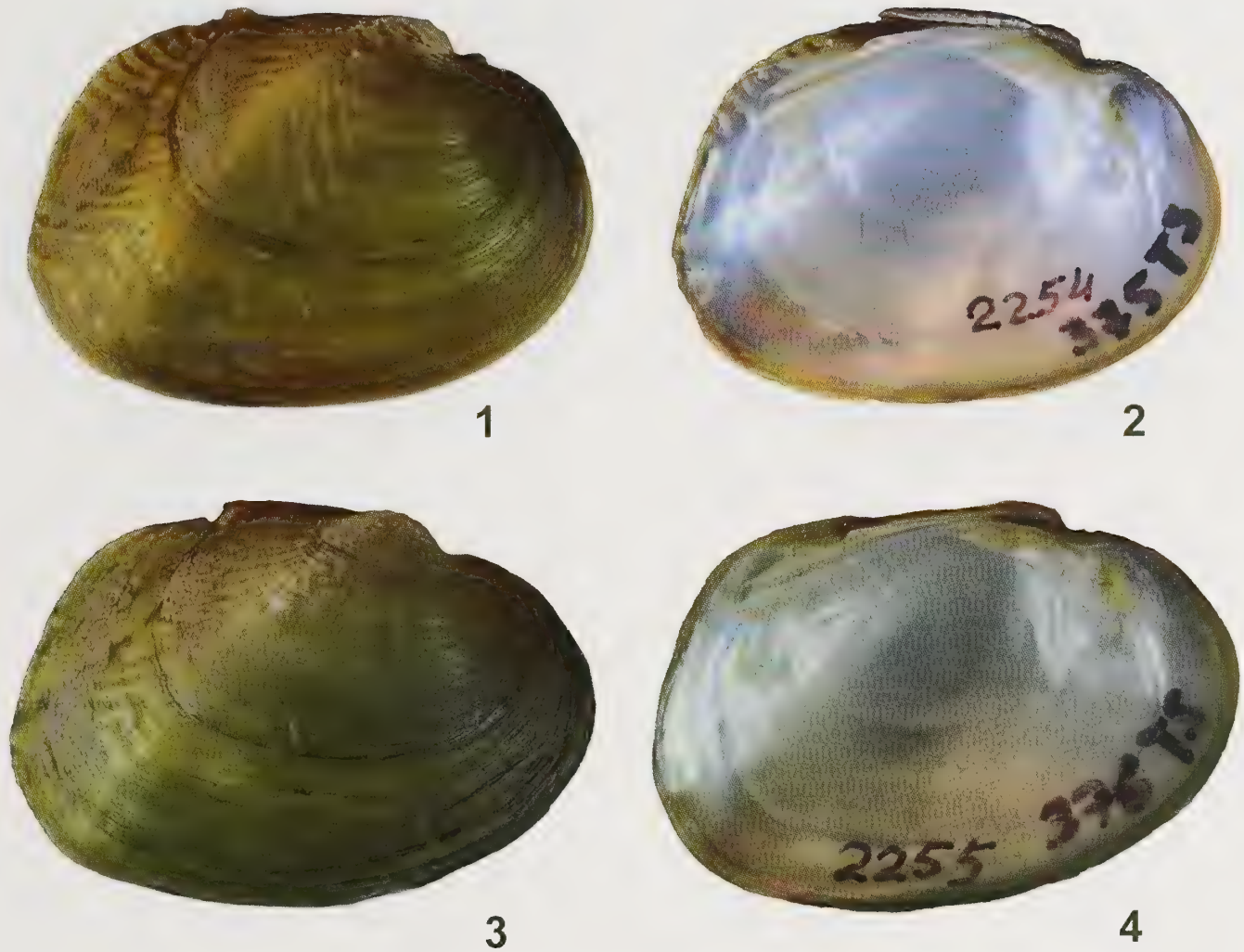
Cyclonaias necki Burlakova, Karatayev, Lopes-Lima, and Bogan new species

Common Name: Guadalupe Orb
(Figures 1–4)

Comparative Diagnosis: Younger shells of *Cyclonaias necki* new species are diagnosed by the distinct corrugations

Table 2. Measurements of *Cyclonaias necki* new species type specimens.

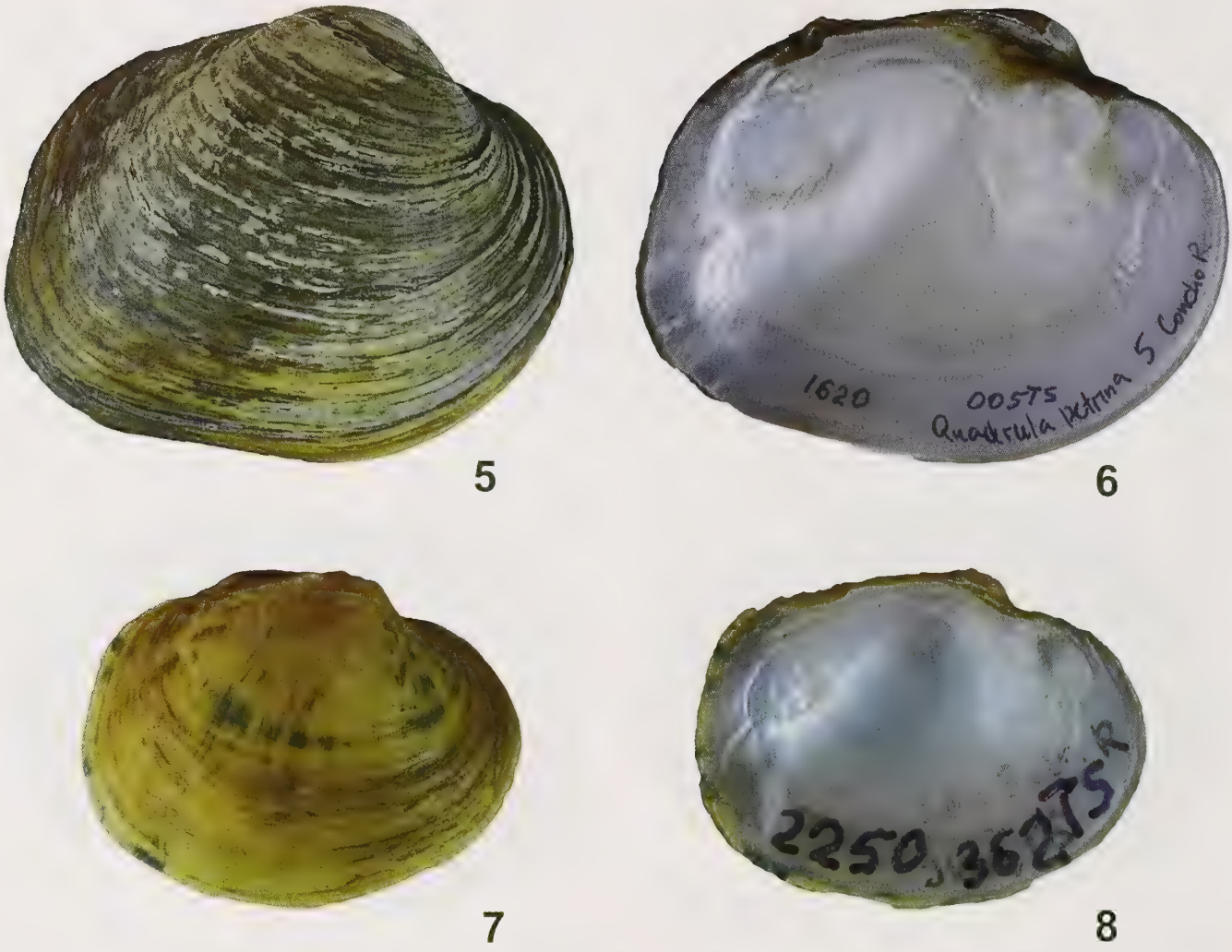
Type	Catalog number	Shell length mm	Shell height mm	Status
Holotype	NCSM 65378	42	30	Live
Paratype	NCSM 65379	60	42	Live
Paratype	BSGLC 2251	63	42	Live
Paratype	BSGLC 2252	58	38	Live
Paratype	BSGLC 2253	54	37	Live
Paratype	BSGLC 2255	43	30	Live
Paratype	BSGLC 2256	45	32	Live
Paratype	BSGLC 2257	40	29	Live
Paratype	BSGLC 2258	47	33	Fresh dead
Paratype	BSGLC 2259	40	28	Fresh dead
Paratype	BSGLC 2260	36	27	Fresh dead



Figures 1–4. *Cyclonaias necki* new species. **1–2.** Holotype NCSM 65378, shell length 42 mm. **1.** Outside of right valve. **2.** Inside of left valve. **3–4.** Paratype BSGLC 2255, shell length 43 mm. **3.** Outside of right valve. **4.** Inside of left valve.

across the posterior slope, extending onto the disk of the shell from the posterior ridge, and lack of pustules (Figures 1–4). *Cyclonaias petrina* (Figures 5–8) has weaker or missing corrugations, typically lack the corrugations on the disk of the shell, and may have occasional pustules. *Cyclonaias petrina* has a thick, inflated shell with a rounded shell disk and round shell shape with an indistinct posterior ridge. Shells of *Cyclonaias necki* new species are thinner, more compressed and rectangular, and the posterior ridge is more distinct and prominent. The umbo on shells of *C. petrina* appears broader and more inflated, while in *C. necki* new species, it is more compressed. Pseudocardinal teeth in *C. petrina* are larger and thicker than in *C. necki* new species. The interdentum of both species are about the same size in relation to shell length. Lateral teeth are short in both species. The umbo cavity of *C. petrina* is deep and open, but appears slightly more compressed in *C. necki* new species. Both species are closely related to *Cyclonaias nodulata* (Rafinesque, 1820), which is very inflated, thick shelled, and usually characterized by two rows of pustules down the disk of the shell, but lacking a sulcus between the rows as seen in *Quadrula quadrula* (Rafinesque, 1820).

Description: Shell length reaches about 63 mm, shell height about 42 mm. Shell shape subquadrate to suboval, shell moderately inflated and relatively thin. Anterior shell margin broadly rounded, dorsal shell margin straight to slightly convex, ventral shell margin slightly convex, posterior shell margin obliquely truncate. Posterior ridge rather well-defined becoming rounded with age. Some specimens have a secondary ridge between posterior ridge and posterior shell margin. Posterior slope covered with fine corrugations running from posterior ridge to posterior shell margin. Umbo area full and well developed, rising above hinge line. Umbo sculpture begins as a series of bars, becomes bumps at either end of a bar, diverging to small bumps down umbo. Periostracum yellowish green to green becoming brown with age, often with fine green rays becoming obscured with age. Shell surface smooth with no pustules, some younger specimens with corrugations extending from posterior ridge anterior ventrally,



Figures 5–8. *Cyclonaias petrina*. **5–6.** BSGLC 1620, shell length 88 mm, Concho River, Concho County, Texas 31.51982N, 099.94063W. **5.** Outside of right valve. **6.** Inside of left valve. **7–8.** BSGLC 2250, San Saba River, San Saba County, Texas, 31.21064N, 098.74124W; shell length 26 mm. **7.** Outside of right valve. **8.** Inside of left valve.

disappearing by central area of shell disk. Sculpture becoming obscured or eroded in older specimens. Single large pseudocardinal tooth in right valve with a vestigial tooth anterior to main tooth, two large sculptured teeth in left valve. Interdentum is well developed in both valves. Lateral tooth single and straight in right valve with two well defined teeth in left valve. Anterior adductor muscle scar deep and smooth, pedal protractor muscle scar deep, separate from, and located posterior and slightly ventral to anterior adductor muscle scar. Anterior pedal retractor muscle scars are deep pits at base of pseudocardinal teeth and almost merge with anterior adductor muscle scar. Posterior adductor muscle scar well defined, but shallow, posterior pedal retractor muscle scar dorsal to posterior adductor muscle scar and merges with posterior adductor muscle scar. Pallial line well defined anteriorly and becoming fainter posteriorly. Umbo cavity deep and open. Nacre color white and iridescent posteriorly.

Type Material: Holotype: NCSM 65378 [ex BSGLC 2254]; **Paratypes:** BSGLC 2251, 2252, 2253, 2255, 2256, 2259, 2260; NCSM 65379 [each lot is a single specimen] (Table 2). All from type locality, collected by Lyubov E. Burlakova, Alexander Y. Karatayev, Vadim A. Karatayev, on July 12, 2011.

Type Locality: San Marcos River, between US90 and SR80, southwest of Luling, Caldwell/Guadalupe counties (the river is the border), Latitude 29.67078 N, Longitude 097.69561 W.

Comparison with Similar Species: *Cyclonaias necki* new species was reported by Strecker (1931) as a small variety, but not separate from *C. petrina*. *Cyclonaias necki* new species was noted by Howells (2013) as "the ecophenotypes in the Guadalupe-San Antonio drainage are often somewhat more elongate, thinner shelled, and with less robust hinge teeth." *Cyclonaias aurea* (Lea, 1859) resembles *C. necki* new species but lacks the corrugations on the posterior slope and the disk of the shell. *Cyclonaias nodulata* (Rafinesque, 1820) is more inflated, thicker

shelled than *C. necki* and is marked by two variable rows of pustules or knobs down the disk of the shell, but lacking a sulcus found in *Quadrula quadrula* and *Q. apiculata* (Say, 1829) and the numerous pustules of these two species. *Cyclonaias necki* new species resembles some *Fusconaia* species, but these species lack the corrugations on the posterior slope.

Molecular Analyses: The COI alignment was 596 base pairs (bp) long and included 7 haplotypes, 4 from the San Antonio/Guadalupe River drainage and 3 from the Colorado River Basin. Two MOTUs were identified by both species delineation methods: one corresponding to the specimens of *Cyclonaias petrina* from the Colorado basin and another corresponding to the specimens of *Cyclonaias necki* new species from the San Marcos River. The interspecific COI divergence (3.9%, uncorrected *p*-distance) is within the usual range for the Unionidae (Prié and Puillandre, 2014; Lopes-Lima et al., 2017). The intraspecific COI divergence within each MOTU was <1%.

Distribution: *Cyclonaias petrina* was recognized from the Colorado River Basin and "A small variety is found in the Guadalupe River in Comal County" was reported by Strecker (1931). It was subsequently reported from the Guadalupe and Colorado River basins and from the Llano, San Saba, and Pedernales rivers (Howells et al., 1996), and recently from the Concho, Guadalupe, San Saba, and San Marcos rivers (Burlakova et al., 2011; Burlakova and Karatayev, unpublished data). The range was listed as "endemic to the Colorado and Guadalupe-San Antonio systems of Central Texas" (Howells, 2013). *Cyclonaias petrina* was recognized by Williams et al. (2017). Here, we have separated *C. necki* new species from *C. petrina* and recognize *C. petrina* as restricted to the Colorado River Basin with *C. necki* new species endemic to the Guadalupe-San Antonio River Basin of Central Texas.

Habitat and Biology: Host fish and the period of gravidity are unknown. *Cyclonaias necki* new species was found living in a small river in flowing water with a sand and gravel substrate, mostly in water less than 2 m.

Conservation Status: *Cyclonaias petrina* was considered threatened (Williams et al., 1993). This new species has been split from *Cyclonaias petrina* which is listed by Texas Parks and Wildlife Department as legally threatened (Howells, 2013). The US Fish and Wildlife Service (USFWS) has been petitioned to examine *C. petrina* for federal listing as threatened or endangered (USFWS, 2018). Their evaluation reported *C. petrina* as having occurred historically in 38 counties, but was listed only from 16 counties today. By recognizing *C. necki* new species from the San Antonio/Guadalupe River Basin, this restricts the modern distribution of *C. petrina* to eight counties in the Colorado River Basin and the range of *C. necki* new species to eight counties. This defines the modern range of *C. petrina* to half of the USFWS listed counties (USFWS, 2018). Considering the restricted range, we would suggest *C. necki* new species and *C. petrina* warrant listing as endangered.

Etymology: We take this opportunity to name the new species, recognizing his work on freshwater mussels of Texas, after Raymond W. Neck, a pleasant and helpful friend (1946–2017).

Comparative Material Examined: Shells of *Cyclonaias petrina* examined for comparison included BSGLC 1620, 2128, 2133, 2156, and NCSM 33710 and 33713.

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First occurrence of the Paleocene gastropod *Ravniella* Rosenkrantz, 1970 (Heterobranchia: Acteonidae) in North America

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ABSTRACT

A new species of the acteonid heterobranch gastropod, ***Ravniella lipmanorum* Squires**, is described from upper lower Paleocene (upper Danian) strata in southern California. This is first record of genus *Ravniella* Rosenkrantz, 1970 in North America. This small-sized genus, which has a broad callus pad bearing two columellar plaits and one parietal plait, is known elsewhere only in Paleocene strata in Denmark, Poland, Austria, and western Greenland. The new species is found mainly at a single locality in the lower part of the Santa Susana Formation, north side of Simi Valley, Ventura County. At this locality, specimens are associated with abundant shallow-marine mollusks, which underwent relatively short-distance, post-mortem transport, probably by turbidity currents emanating from shallower marine depths. The new species is found rarely in the lower part of the San Francisquito Formation, Warm Springs Mountain area, Los Angeles County. *Ravniella* occurs questionably in Upper Cretaceous strata of northern Spain (Campanian). **The senior author, Squires, is the sole author of the new species.**

Additional Keywords: Tornatellaea, *Ringicula*, paleobiogeography

INTRODUCTION

Since at least the Late Triassic, shell-bearing "lower heterobranch" gastropods, which were traditionally referred to as shelled "opisthobranchs," have been an important component of shallow-marine gastropod faunas (Gründel and Nützel, 2012). Today "lower heterobranchs" represent one of the most diverse lineages in Mollusca, but evolutionary relationships remain incomplete (Kano et al., 2016). One of the earliest "lower heterobranch" groups is family Acteonidae d'Orbigny, 1842, which first appeared during the Middle Jurassic in Europe (Gründel et al., 2012). Modern-day acteonids prey mainly on polychaete worms, to such an extent that, according to Helwerda (2015), the presence of acteonids in an area indicates that polychaete worms must also be present. Yonow (1989) reported on a modern-day acteonid, which is a specialized vermivore, feeding only on tube-dwelling polychaete worms. This acteonid crawls along the surface of patches of clean, well-sorted, medium to fine sand, and, upon detecting its prey, burrows 5 to 10 cm to reach the worm tube.

This present paper concerns the recent discovery of a new species of the acteonid genus *Ravniella* Rosenkrantz (1970) from lower Paleocene rocks at two localities in southern California. *Ravniella* has been traditionally a subgenus of *Tornatellaea* Conrad, 1860, but some workers (e.g., Kollmann and Peel, 1983; Schnetler, 2001; Blagovetshenskiy, 2017) used *Ravniella* as a distinct genus. None, however, described, in detail, how *Ravniella* differs from *Tornatellaea*. These differences are given here. The discovery of the new species, ***Ravinella lipmanorum* Squires**, is significant because this genus had been found before only in Paleocene rocks in western Europe and western Greenland.

Most specimens of the new species are from the lower Santa Susana Formation in northern Simi Valley, Ventura County, southern California, but two are from the lower San Francisquito Formation, Warm Springs Mountain area, Los Angeles County, southern California (Figure 1). The new species most likely inhabited nearshore-marine depths but underwent post-mortem transport into deeper waters. **The senior author, Squires, is the sole author of this new species.**

MATERIALS AND METHODS

The new species is based on 44 specimens stored in the Invertebrate Paleontology Collection of the Natural History Museum of Los Angeles County (LACMIP). Details about the localities of the new species are given in Appendix 1. Most of the specimens were found in Simi Valley at LACMIP locality 41691, discovered by the junior

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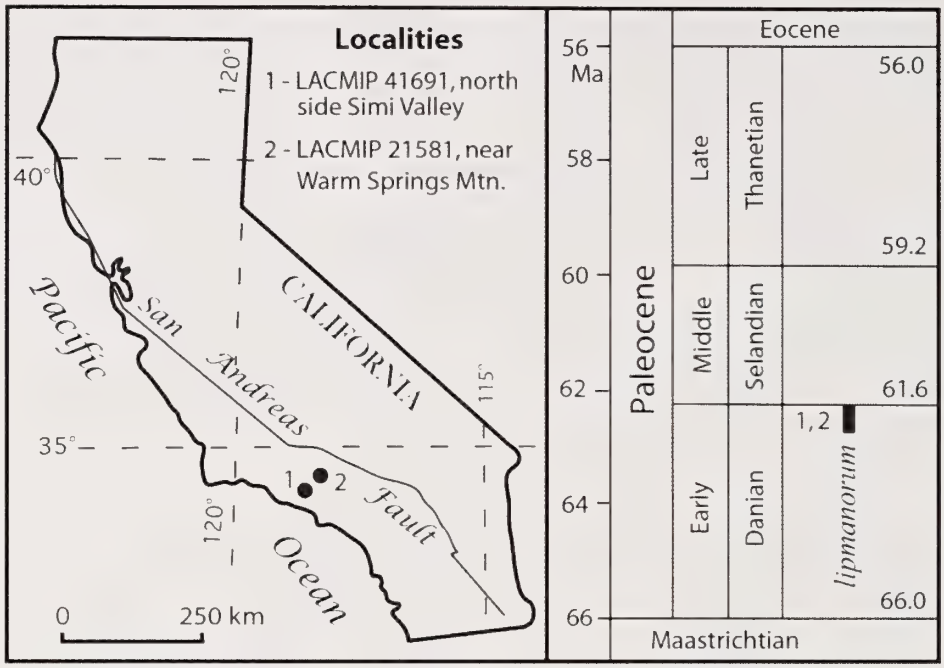


Figure 1. Localities map and chronostratigraphy of ***Ravniella lipmanorum* new species Squires**. Ages from Gradstein et al. (2012).

author in 2015, when he was prospecting for fossils in an area undergoing construction of a road, to provide access to a planned development of nearby homesites. A search of the LACMIP Collection yielded two additional specimens of the new species. They were found by an early collector, in the 1940s, in the Warm Springs Mountain area (see Appendix 1).

Cleaning of apertures was done by careful use of very sharp needles. The classification system of Bouchet et al. (2017) is followed here, but "categories" higher than superfamily remain mostly in a state of flux. General morphologic terms are from Cox (1960), and protoconch terminology is from Schröder (1995).

STRATIGRAPHY, DEPOSITIONAL ENVIRONMENTS, AND AGES

Nearly all the specimens are from LACMIP loc. 41691, in the lower part of the Santa Susana Formation, on the north side of Simi Valley, southern California. As recognized by Parker (1981: fig. 4), this formation consists of an "eastern facies" (mostly slope and inner-fan turbidite deposits) and a "western facies" (nearshore to offshore deposits). Fossils at locality 41691 occur in the "eastern facies," which typically contains sparse macrofossils. Fossils at this locality are, however, unusually abundant. They are in float derived from a nearly completely covered, approximately 25 cm-thick *Turritella*-rich storm bed which caps a low hill consisting of 30 m of of black silty mudstone, which weathers gray. Based on a few scattered pieces of rock in the float, it can be determined that this storm bed consists of fossiliferous sandstone, with some very rare small-cobble clasts. In addition to the very abundant *Turritella peninsularis quaylei* Saul, 1983, there is a diverse assemblage of other gastropods at this locality, as well as some bivalves (rarely with conjoined valves), boring bivalves (in wood), solitary corals, colonial corals (very rare), raninid crabs, spiny lobster fragments, echinoid spines, and petrified wood (Squires et al., in press). All these fossils were likely swept from various relatively shallow depths by channelized debris flows, then transported and concentrated on the adjacent slope (Parker, 1981; Squires et al., in press). Although most of the *Turritella* specimens consist of only the upper spire, they are not worn nor abraded. Also, the presence of protoconchs and delicate sculpture on some of the gastropods is evidence that the distance of postmortem transport was not great. Based on concurrent ranges of various species of *Turritella* and other gastropods, the rocks at the Simi Valley locality are of late early Paleocene age (late Danian Stage) (Squires et al., in press).

Only two specimens are known from East Fork Fish Canyon, just west of Warm Springs Mountain area (see Saul, 1983: fig. 13), in the lower part of the San Francisquito Formation at LACMIP loc. 21581. The fossils, which are in black siltstone, consist of *Turritella peninsularis quaylei* and a moderate diversity of other gastropods and some bivalves. Based on the presence of *T. p. quaylei*, the age of the rocks at this locality is the same as for the above-mentioned LACMIP loc. 41691.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia
Grade "Lower Heterobranchia"
Infraclass Euthyneura

Cohort Acteonimorpha
Superfamily Acteonoidea d'Orbigny, 1842

Discussion: Acteonoid euthyneuran gastropods were traditionally considered to be basal members of an enigmatic group referred to as the shelled "opisthobranchs" (e.g., "bubble snails") (Kano et al., 2016). Molecular phylogeny studies, in combination with anatomical and cladistic studies, show that "bubble snails" have polyphyletic status (Mikkelsen, 2002). They have uncertain systematic affinity and might have a basal placement outside of the "opisthobranchs," or they might have an "opisthobranch" origin (Göbbeler and Klussmann-Kolb, 2010).
Family Acteonidae d'Orbigny, 1842

Genus *Ravinella* Rosenkrantz, 1970

Type Species: *Cinulia danica* Ravn, 1902, by original designation; early Paleocene, Danian Stage, Denmark.

Description: Shell small sized, commonly 8 to 10 mm height (rarely up to 13.5 mm height). Height/width ratio 1.5 to 1.8. Oval, moderately inflated to tumid. Spire moderately low; upper spire can be tilted slightly. Spire angle 70° to 87°. Protoconch approximately 1.5 whorls, paucispiral, smooth, heterostrophic, and coaxial. Teleoconch four to five whorls. Whorls convex. Suture impressed, slightly channeled. Spiral grooves very narrow and pitted; interspaces smooth, moderately wide to wide. Aperture narrow to wide; anterior end moderately narrow to patulous.

Callus pad (inductura) along inner lip well developed and well delineated. Anterior part of callus pad crenulate and bearing two, commonly wide and equally to subequally stout columellar plaits, both lowly to moderately oblique, with posterior one very commonly longer. Adaxial end of columellar plaits commonly swollen and deflected backward. Parietal callus pad narrow (commonly) or broad; parietal-plait area extending from medial-basal part of last whorl to low or sharp angulation, at where callus pad bends abruptly apexward along upper inner lip. Parietal plait short or long, nearly horizontal to lowly oblique. At or near where bending of callus occurs, parietal plait can be either bifurcated, or single pustule, or small swollen area (nearly smooth). Outer lip edge thick; subadjacent shell can be varicose. Outer lip interior smooth or with several lirae or denticles, both becoming obsolete anteriorward. Growth line very slightly opisthocline.

Geologic Age: Campanian (questionably); late early Paleocene (late Danian) to late Paleocene (Thanetian).

Discussion: Rosenkrantz (1970: 431) initially reported *Ravniella* to be a subgenus of *Tornatellaea* Conrad, 1860, a gastropod which ranges from early Middle Jurassic (Gründel et al., 2012) to early Oligocene (MacNeil and Dockery, 1984), and, according to Kaim (2004: 168) is the earliest known member of family Acetonidae. *Ravniella* is a genus similar to but distinct from *Tornatellaea*. *Ravniella* has a lower spire, wider spiral angle, more tumid last whorl, much less oblique and much stouter columellar plaits, a parietal plait (which can be incipient), as well as the possibility of having lirae or denticles on the interior of the outer lip.

All the known species of *Ravniella* are listed in Table 1. All except the new species are found only in Western Europe or western Greenland. *Ravniella danica* (Ravn, 1902: 34–35, pl. 3, fig. 7; Rosenkrantz, 1970: fig. 10.1) is from the *Cerithium* limestone, Stevns Klint, Denmark. *Ravniella groenlandica* Rosenkrantz, 1970: fig. 10.2; Kollmann and Peel, 1983: 105, fig. 242) is from the *Propeamussium* Member (a black mudstone) of the Kangilia Formation [now referred to as the Eqalukik Formation, according to Dam et al. (2009)], Nugssauaq Peninsula, central western coast of Greenland. *Ravniella regularis* (von Koenen, 1885: 76, pl. 3, figs. 24a–c; Rosenkrantz, 1970: fig. 10.4) is from Copenhagen, Denmark. *Ravniella* aff. *regularis* (von Koenen, 1885; Rosenkrantz, 1970: fig.10.3) is from the Agatdal Formation, Sonja lens (a black shale), Nugssuaq Peninsula, central coast of western Greenland. *Ravniella rosenkrantzi* Traub (1989: 100–101, pl, 3, figs. 4a–b, 5a–b) is from the Kroisbach Member of the basal part of the Kressenberg Formation, Haunsberg area near Salzburg, Austria. *Ravniella "inopinata"* Morlet (1888: 329–330, pl. 13, figs. 8–10) *sensu* Krach (1963: 138–139, pl. 15, figs. 4, 4a) [misidentified by Krach, as to species] is from the Babica Clays, Middle Carpathian Mountains, southeastern Poland.

Tornatellaea sp. 1 and sp. 2 of Kiel and Bandel (2001: 326, pl. 2, figs. 14–17) from Upper Cretaceous (Campanian) strata in northern Spain, are similar to *Ravniella*,

Table 1. Ages and geographic distribution of known and questionable species of *Ravniella*.

Species	Age	Location
R. "inopinata" sensu Krach, 1963	Thanetian	Southeastern Poland
R. regularis (von Koenen, 1885)	early Selandian	Denmark
R. rosenkrantzi (Traub, 1989)	late Danian; late Thanetian	Austria
***R. lipmanorum* Squires new species**	late Danian	Southern California
R. aff. *regularis* (von Koenen, 1885)	late Danian	Western Greenland
R. groenlandica Rosenkrantz, 1970	early Danian	West Greenland
R. danica (Ravn, 1902)	earliest Danian	Denmark
R.? spp. (Kiel and Bandel, 2001)	Campanian	Northern Spain

in shape, size, sculpture, two strong columellar plaits, and weak presence of a parietal plait. These two unnamed species, which might be conspecific (Kiel and Bandel, 2001), are reported here for the first time, as the earliest questionable representative of *Ravinella* in the fossil record (Table 1).

Rosenkrantz (1970) did not provide a full description of *Ravniella* nor did he discuss any morphologic details of the parietal plait, especially the morphologic variation displayed in his illustrations (fig. 10, 1–4) of several different species of this genus. This variation includes a short, horizontal plait where the callus pad bends apexward along the upper lip (fig. 10.1), a protuberance where the oblique callus pad bends apexward along the upper inner lip (fig. 10.2), a moderately long, lowly oblique, ridge-like thickening (fig. 10.3), and a nearly horizontal angulate to ridge-like thickening where the callus pad bends apexward along the adapical margin of the inner lip (fig. 10.4). Rosenkrantz (1970) also did not describe the protoconch of *Ravniella*, but his sketches of *Ravniella danica* and *Ravniella regularis* (von Koenen, 1885) show a small, paucispiral heterostrophic protoconch (see Rosenkranz, 1970: figs. 10.1, 10.4).

Ravniella is somewhat similar to the acteonid *Vasjugania* Kaim and Beisel (2005: 57–58, fig. 15), of Maastrichtian age from western Siberia, Russia, in terms of having a parietal plate in addition to columellar plaits. *Ravniella* differs by having only two columellar plaits, rather than three, a more tumid last whorl, pitted spirals with wider interspaces, lirate or dentate outer lip interior, and a tapered anterior end of the aperture. The high, narrow spire of *Vasjugania* is similar to *Tornatellaea*. Kaim and Beisel (2005) reported that *Acteon ringens* d'Orbigny (1842: 121–122, pl. 167, figs. 13–15), from Lower Cretaceous Hauterivian strata in France, also belongs to *Vasjugania*, and d'Orbigny's species has a much lower spire and a more tumid last whorl, like that of *Ravninella*. All these observations serve to show that the evolution of *Ravniella*, *Tornatellaea*, and *Vasjugania* need further study.

Ravniella is similar also to *Ringicula* Deshayes, 1838, which, according to Kaim (2014: 154–155, has been mistakenly identified, by some authors, as *Tornatellaea*. *Ringicula* belongs to the shell-bearing "lower heterobranch" family Ringiculidae Philippi, 1853, which might have evolved from *Tornatellaea*-like acteonids (Kaim, 2004: 166, fig. 140). *Ringicula* ranges from late early Middle Jurassic (Callovian) to Recent (Kaim, 2004: 156). *Ringicula*, like *Ravniella*, also has two columellar plaits and a parietal plait, which is variable in its shape, but *Ringicula* differs by possibly having a partially impressed initial protoconch whorl, commonly having a smooth globose to subglobose shell, a lower spire, heavily callused inner lip, very thick outer lip (can be smooth within) that extends more posteriorward, and a notched anterior peristome (Sohl, 1964: 293; Kaim, 2004: 156, 169).

Ravniella resembles somewhat the euthyneuran *Triploca* Tate, 1893, of Eocene age from Australia, but *Triploca* has three columellar plaits. They are all positioned in the anterior end of the shell and are equidistantly located, as well as being approximately the same size.

Adegoke (1973: fig. 5; 1977: 215–216, pl. 32, figs. 22–26) illustrated an acteonid gastropod which he identified as *Tornatellaea* (*Ravniella*) *africana* Furon, 1948 [in Furon and Kouriatchy, 1948]. Based on its a high spire, nearly vertical to oblique columellar plaits, absence of a parietal plate, and no sculpture on the interior of its outer lip, Furon's species does not belong to *Ravniella*.

***Ravniella lipmanorum* new species Squires**
(Figures 2–14)

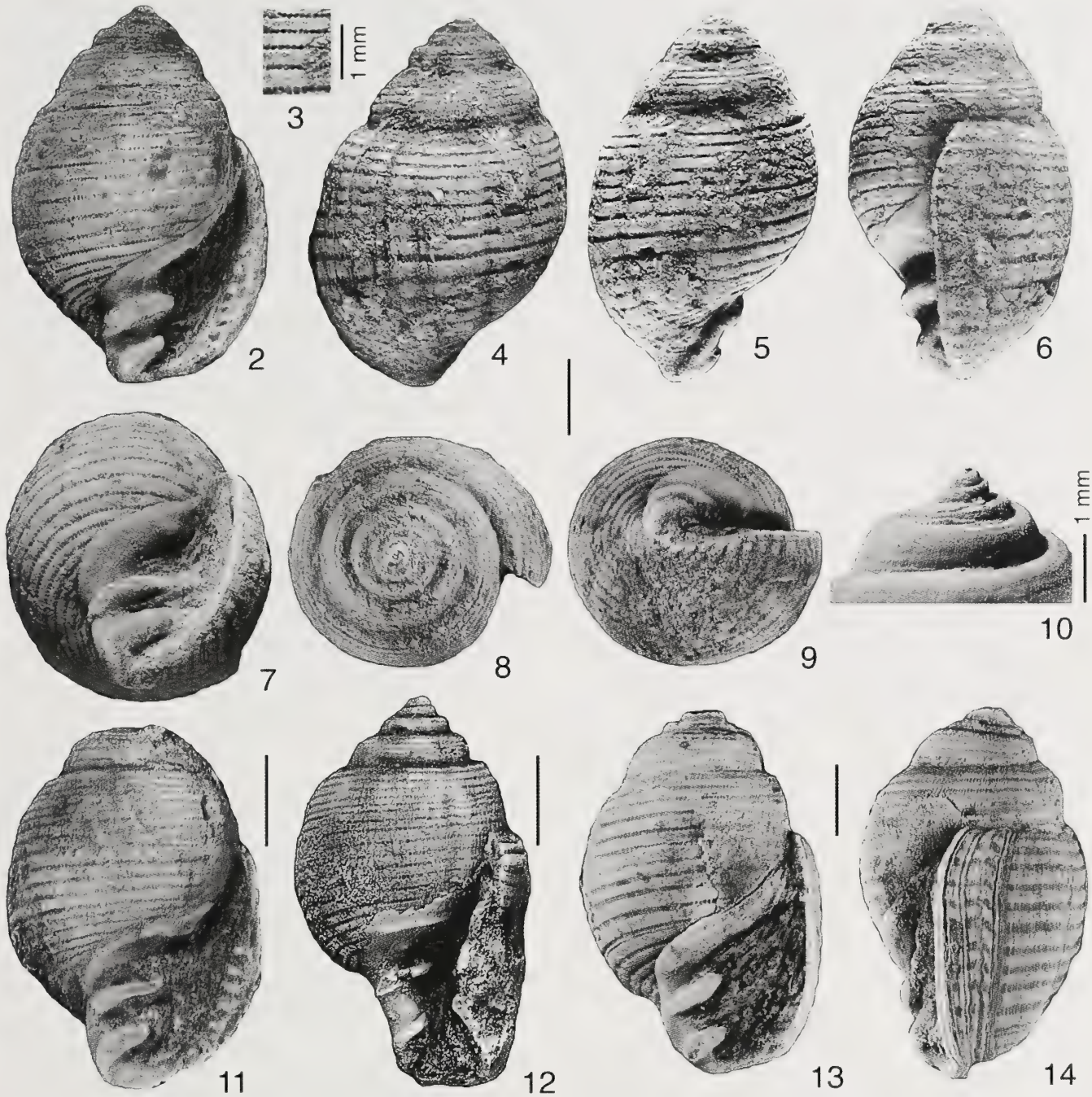
Tornatellaea n. sp.—Squires et al., in press.

Diagnosis: *Ravniella* with wide spire angle (80° to 86°), narrow aperture, spiral grooves separated by much wider areas, denticles (not lirae) on outer lip interior.

Description: Shell commonly 9 to 10 mm height and 6 to 7 mm width; (rarely up to 11.5 mm height and 6.3 mm width); height to width ratio commonly 1.5 to 1.6 (rarely 1.8). Oval, tumid. Spire moderately low; upper spire can be tilted slightly. Height of spire less than height of aperture. Spire angle 80 to 86°. Protoconch heterostrophic, coaxial, and tilted. Teleoconch with up to approximately four convex whorls. Suture impressed to slighly channeled; ramp small, can be somewhat angulate. Sculpture comprised of very narrow, incised spiral grooves, continuous, and crossed by collabral microscopic bars (growth lines), forming cells made minutely pitted by constriction at regular intervals. Spiral grooves separated by much wider, flat smooth areas, widest on periphery of last whorl and becoming narrow on neck. Aperture elongate, narrow, and widening slightly anteriorly. Callus pad (inductura) on columella area bearing two lowly oblique plaits, equally to subequally thick (rarely thin), and crenulate; posterior plait can extend slightly farther into aperture. Callus pad on parietal area prominent, broad, extending obliquely onto base of last whorl and abruptly bending apexward to posterior end of inner lip or near it. Parietal callus broad and can be slightly detached. Parietal-plait area extending from medial-basal part of last whorl to low or sharp angulation, at where callus pad bends abruptly apexward along upper inner lip. Parietal plait short or long, nearly horizontal to lowly oblique. At or near where bending of callus occurs, parietal plait can be either bifurcated, or single pustule, or small swollen area (nearly smooth). Umbilical groove weak, partly obscured in apertural view by the columella. Outer lip interior can be thickened and bearing approximately seven moderately widely spaced denticles; exterior area adjacent to outer lip edge can be varicose. Growth line slightly inclined (opisthogryral) and with small deflection near suture. Growth lines can be prominent (varicate) and closely spaced in vicinity of exterior edge of outer lip.

Holotype: LACMIP 14724, 10.6 mm height and 7.3 mm width (protoconch incomplete), height to width ratio 1.5 (Figures 2–9).

Paratypes: LACMIP 14725–14728.



Figures 2–14. ***Ravniella lipmanorum*** **new species Squires**, LACMIP loc. 41691, lower Santa Susana Formation. Specimens whitened with ammonium chloride. **2–9.** Holotype LACMIP 14724. **2.** Apertural view. **3.** Apertural view, closeup of spiral grooves on upper right part of last whorl. **4.** Abapertural view. **5.** Left-lateral view. **6.** Right-lateral view. **7.** Oblique view of anterior end of last whorl. **8.** Apical view. **9.** Abapical view. **10.** Paratype LACMIP 14725, abapertural view of last whorl of teleoconch and apertural view of hyperstrophic protoconch. **11.** Paratype LACMIP 14726, apertural view. **12.** Paratype LACMIP 14727, apertural view. **13–14.** Paratype LACMIP 14728. **13.** Apertural view. **14.** Right-lateral view. Scale bars = 2 mm, unless otherwise indicated.

Type Locality: LACMIP 41691. The locality, which is on private property, was temporary. It is now covered by the installment of landscaping and sprinklers.

Geologic Age: Late early Paleocene (late Danian).

Distribution: San Francisquito Formation, East Fork Fish Canyon, Warm Springs Mountain, Los Angeles Co., southern California; lower Santa Susana Formation, just south of Mount Sinai Memorial, north side of Simi Valley, Ventura Co., Southern California.

Etymology: The new species is named for the Paul Lipman family, in recognition of their discovery of the locality and careful collecting of specimens, which they

kindly donated. **The senior author, Squires, is the sole author of this new species.**

Discussion: Forty-four specimens were examined, and all, but two, are from LACMIP loc. 41691. About 20 specimens from this locality have good to very good preservation, including presence of the protoconch. On all of these 20 specimens, however, the shell material of the protoconch has been decorticated, leaving only an internal cast showing the shape of the protoconch. This shape matches closely with the shape of the protoconch of *Tornatellaea* illustrated by Kaim (2004: figs. 132–133). A few mature specimens of the new species from the lower Santa Susana Formation have one or two narrow radial furrows on the last whorl, and these are secondary in origin. The two specimens from the lower San Francisquito Formation have moderately poor preservation, including absence of a protoconch.

The new species is the first occurrence of *Ravniella* in the fossil record of the northeast Pacific. Compared to the known species of *Ravniella*, the new species differs by having a wider spiral angle, narrower aperture, and denticles on the outer lip interior. *Ravniella lipmanorum* is most similar to *Ravniella danica* (Ravn, 1902: 238–239, pl. 3, fig. 7; Rosenkrantz, 1970: fig. 10.1) from lowermost Danian strata in Denmark. The new species differs by having upper spire whorls slightly tilted on some specimens, callus pad on parietal area commonly wider, more variable development of the parietal plait, and presence of denticles rather than long lirae on the outer lip interior. *Ravniella lipmanorum* is also very similar to *Ravniella groenlandica* (Rosenkrantz) of Kollmann and Peel, 1983: 105, fig. 242 [= *Ravniella* aff. *R. groenlandica* Rosenkrantz, 1970: fig. 10.2] from lower Danian strata in western Greenland. The new species differs by smaller maximum size, less tumid, wider spiral angle, narrower aperture, narrower and not upturned columellar plaits, parietal-area callus pad commonly wider, and more dentate outer lip interior.

PALEOBIOGEOGRAPHIC CONSIDERATIONS

The early Paleocene (early Danian) occurrence of *Ravniella* in Denmark is the earliest unequivocal record of this genus. From Denmark, the genus spread to southeastern Poland, Austria, western Greenland, and, by the late Paleocene, into southern California. During Paleocene and Eocene time, the paleoclimate of the west coast of North America was warm temperate, and during this interval there were pulses of immigration of many shallow-marine, thermophilic mollusks, with most arriving from the Old World Tethyan Sea region via westward-flowing currents that passed through a low-latitude seaway in southern Mexico (Squires, 1987, 2003). The arrival of *Ravniella* into southern California was most likely via one of these west-trending immigration pulses in equatorial waters. The long distance involved and the relatively short duration (approximately four million years) for this dispersal of *Ravniella* argue for a planktotrophic larval stage.

It is possible that *Ravniella* originated earlier, however, during the Late Cretaceous in Spain, thereby allowing for more time for westward dispersal. This scenario is supported by the questionable occurrence of Late Cretaceous (Campanian) specimens of *Ravniella* in northern Spain.

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APPENDIX 1

LOCALITIES OF THE NEW SPECIES

All quadrangles listed below are U. S. Geological Survey, 7.5 minute, topographic maps.

LACMIP 21581. North of truck trail in small unnamed canyon west of Rattlesnake Canyon, 34°37'20.75"N, 118°37'21.49"W, elevation 2660 feet, lower San Francisquito Formation, north side of East Fork Fish Canyon, Los Angeles Co., southern California, Warm Springs Mountain Quadrangle. Age: Late early Paleocene. Collectors: E. H. Quayle, June, 1941.

LACMIP 41691. Temporary exposure made during construction of Mount Sinai Road, 34°13'12.02"N, 118°40'3.63"W, elevation 1220 feet, lower Santa Susana Formation, north side of Simi Valley, Ventura County, southern California, Santa Susana Quadrangle. Age: Late early Paleocene. Collectors: P. Lipman, Jacob Lipman, R. L. Squires, 2015–2017.

A new species of *Calliostoma* (Gastropoda: Calliostomatidae) from Weizhou Island, South China Sea

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ABSTRACT

This paper describes and illustrates *Calliostoma spesa* new species, sampled from the intertidal zone in coarse sandy bottom in Weizhou Island, the South China Sea. The new species is characterized by its conical shell with dense spiral cords which are composed by strings of strong beads. We describe the shell characters in detail and compare it with the similar species *Calliostoma basulense* Poppe, Tagaro and Vilvens, 2014. Mitochondrial 16S rRNA and nuclear 28S rRNA genes of the new species are sequenced. Phylogenetic trees constructed using Bayesian inference (BI) and maximum likelihood (ML) analyses incorporating available *Calliostoma* sequences from GenBank, confirm the generic assignment of this taxon to a new species.

Additional Keywords: Trochoidea, *Calliostoma*, taxonomy, phylogeny, 16S, 28S, Beibu Gulf

INTRODUCTION

Calliostomatidae is a basal family in Gastropoda, occurring in the tropics, subtropics, temperate zones, and polar regions, from intertidal and subtidal to several thousand meters deep on sandy, muddy, or rocky substrates. Calliostomatids are small (a few mm) to rather large (up to 80 mm) in size, conical, cyrtoconoidal, or coeloconoidal in shape. Shells of members of this family usually have strong spiral cords, usually with bead-like or knob-like nodules or small spines on cords, a protoconch sculptured with a network of threads forming polygonal spaces, a convex to flat base with spiral cords, and a corneous, subcircular operculum with a subcentral nucleus. Marshall (2016) estimated that this family is represented by more than 300 recent species worldwide. According to WoRMS (World Register of Marine Species) and MolluscaBase, about 440 recent valid species in about 30 accepted genera are on record at the time of writing (MolluscaBase, 2018).

This family is well studied in the southwest Pacific. In 1995, Marshall conducted two important systematic works. A total of 30 species, including 27 new species, from New Caledonia (Marshall, 1995a) and 33 species, including 10 new species, from New Zealand (Marshall, 1995b) were studied in detail. Some of the taxa within this group were revised, discriminated, and delimited. Since then, great attention has been devoted to this group. Systematic studies and new species are coming forth, continuously, especially on species from tropical Pacific islands. Vilvens recorded 13 species, including 5 new, from Vanuatu, Fiji, and Tonga (Vilvens, 2005), and 16 species, including 7 new, from New Caledonia and the Solomon Islands (Vilvens, 2009). Stratmann and Schwabe (2007) described another new species, also from the Solomon Islands. Marshall (2016) described 3 new species from New Zealand and reported a new record from the latter islands.

The Philippines is another biodiversity hotspot for Calliostomatidae. In total, 33 calliostomatids have been reported from there (Poppe, 2008; 2011; 2017), with many new species described (Bozzetti, 1997; Vilvens, 2000a; 2000b; Poppe, 2004; Poppe, et al., 2006; Poppe, et al., 2014). In the northwest Pacific, 29 species are recorded from Japan (Sasaki, 2017). Despite the lack of extensive studies covering Chinese waters, Dong (2002) conducted systematic studies on the superfamily Trochoidea of China. He reported only 11 species from 2 genera within the Calliostomatidae, including 2 new to science. Fu (2007) reported 8 species from Taiwan. Zhang (2008) recorded 12 species and 2 genera from Chinese

seas. Huang and Fu (2015) described 2 new species from Taiwan and the Yellow Sea. Most numbers of this family in China are distributed in the East China Sea and South China Sea, except 3 living in the Bohai Sea and Yellow Sea. There should be more species waiting for their discovery.

Recent phylogenetic studies of the Calliostomatidae supported by morphological and molecular studies accept the inclusion of five subfamilies (Williams, 2012; Marshall, 2016). But the relationships at the generic level have not yet been well defined, most likely because of extensive variations in shell morphology and inadequate sampling for thorough genetic studies. Many genera or subgenera have been erected or separated from the type genus *Calliostoma* Swainson, 1840. But some are not widely accepted or are still in dispute. Accordingly, quite a few species, including some recently described, are lumped in the genus *Calliostoma*, when it is clear that they should belong in a different genus-level taxon. Although more and more species within *Calliostoma* have been discovered since 1995, genetic information is still insufficient to solve the generic relationships.

Specimens of two individuals were collected in May 2016, from the intertidal zone of Weizhou Island, located in the Beibu Gulf, South China Sea, under the jurisdiction of Guangxi Zhuang Autonomous Region, China. Our initial studies indicated that these samples belong to a new species.

MATERIALS AND METHODS

Two individuals of the new species were collected. The larger one was well-developed empty shell, here assigned as the holotype of the new species. The smaller one was sampled alive, preserved in 70% ethanol for molecular analyses, and is here designated as the only paratype of the new species. Shells were observed under light microscopy and photos were taken using a Cannon EOS6D camera. Images of the protoconch were captured under a Zeiss Discovery V12 stereo microscope using a Zeiss AxioCam 503 digital camera. Measurements were made with a vernier caliper to the nearest 0.1 mm. Spiral cords on shell are numbered consecutively adapically to abapically following Ikebe (1942), Marshall (1988) and Vilvens (2009).

Total DNA was extracted using the Marine Animal Genomic DNA Extraction Kit (Tiangen Biotech, Beijing,

Table 1. List of species and their GenBank accession numbers of sequences used in present study.

Species	28S rRNA	16S rRNA
Calliostoma aculeatum Sowerby III, 1912[1]	AB505225	AB505316
Calliostoma akoya (Kuroda in Ikebe, 1942)	AB505226	AB505317
Calliostoma antonii (Koch in Philippi, 1843)	GQ160645	GQ160691
Calliostoma antonii (Koch in Philippi, 1843)	GQ232378	GQ232281
Calliostoma consors (Lischke, 1872)[1]	EU530015	–
Calliostoma consors (Lischke, 1872)[1]	GQ232388	GQ232289
Calliostoma granulatum (Born, 1778)	–	DQ093478
Calliostoma granti (Powell, 1931)	GQ249711	–
Calliostoma haliarchus (Melvill, 1889)[1]	AB505227	AB505318
Calliostoma iridium (Dall, 1896)	GQ232380	GQ232283
Calliostoma javanicum (Lamarck, 1822)	EU530014	–
Calliostoma jujubinum (Gmelin, 1791)	GQ232381	–
Calliostoma kiheiziebisu (Otsuka, 1939)[2]	AB505228	AB505319
Calliostoma ligatum (Gould, 1849)	GQ232383	GQ232285
Calliostoma multiliratum (Sowerby II, 1875)	AB505229	AB505320
Calliostoma punctulatum (Martyn, 1784)	GQ249708	GQ249817
Calliostoma punctulatum (Martyn, 1784)	–	GQ249820
Calliostoma shinagawaense Tokunaga, 1906[3]	AB505230	AB505321
Calliostoma tigris (Gmelin, 1791)[4]	GQ249709	GQ249818
Calliostoma torrei Clench & Aguayo, 1940	–	DQ314294
Calliostoma torrei Clench & Aguayo, 1940	–	KY671200
Calliostoma unicum (Dunker, 1860)[3]	AB505231	AB505322
Calliostoma waikanae (Oliver, 1926)[4]	GQ249710	GQ249821
Calliostoma zizyphinum (Linnaeus, 1758)	EU530016	–
Calliostoma zizyphinum (Linnaeus, 1758)	–	KY200894
Calliostoma spesa new species	MH444454	MH444453
Margarella antarctica (Lamy, 1905)	GQ232398	–
Margarella biconica (Numanami, 1996)	HE800692	HE800741
Margarella crebrilirulata (Smith, 1907)	HE800693	HE800742
Margarella refulgens (Smith, 1907)	HE800694	HE800743

[1] Belongs to the genus *Tristichotrochus* Ikebe, 1942 (*fide* WoRMS, 2018)
[2] Belongs to the genus *Otukaia* Ikebe, 1942 (*fide* WoRMS, 2018)
[3] Belongs to the genus *Tristichotrochus* Ikebe, 1942 (*fide* WoRMS, 2018)
[4] Belongs to the genus *Maurea* Oliver, 1926 (*fide* WoRMS, 2018)

China). Fragments of the mitochondrial 16S rRNA gene were amplified using 16Sa: 5′-CGC CTG TTT ATC AAA AAC AT-3′ (Xiong and Kocher, 1991), 16Sb: 5′-CTC CGG TTT GAACTC AGA TCA-3′ (Edgecombe, Giribet, and Wheeler, 2002). The nuclear 28S rRNA gene was amplified using 28S-D1F: 5′-GGG ACT ACC CCC TGA ATT TAA GCA T-3′, 28S-D6R: 5′-CCA GCT ATC CTG AGG GAA ACT TCG-3′ (Park and Ó Foighil, 2000). The 25-μL reaction for the amplification contained 12 μL 2×Es TaqMasterMix (CWBio Co., Ltd, Beijing, China), 2 μL of template DNA (50 ng/μL), 1 μL of each primer (10 M) and 9 μL dH_2O. Amplification reactions were conducted in a T100 Thermal Cycler (Bio-Rad Laboratories, Inc.) with the following thermal profile: 95°C for 3 min; 35 cycles of 95°C for 30 s, 48–52°C for 45 s, 72°C for 1 min, and a further 10-min elongation at 72°C. The PCR products were purified and sequenced by BGI Tech Solutions Co., Ltd. One partial 16S sequence and one 28S sequence were obtained and have been deposited in GenBank. For phylogenetic analyses, some of the

Figures 1–7. *Calliostoma spesa* new species. **1–4. Holotype, MBM229029. 1.** Apertural view. **2.** Dorsal view. **3.** Adapical view. **4.** Protoconch. **5–7. Paratype, XSM unnumbered. 5.** Apertural view. **6.** Dorsal view. **7.** Paratype, alive.

sequences used here were retrieved from GenBank (see Table 1). Species of *Margarella*, subfamily Margarellinae Williams, 2013 were selected as outgroup. Sequences were aligned independently using MAFFT v.7 (Katoh and Standley, 2013) with the G-INS-i algorithms for the protein-coding and ribosomal regions. Maximum likelihood (ML) analysis was carried out using RAxML 8.1.2 (Stamatakis, 2014) (with bootstrapping) using GTR+G+I as the model for each partition on combined data. Bayesian inference was done using the software MrBayes 3.2.6 (Ronquist et al., 2012). Analyses were run for 10 million generations using four chains with a sampling frequency of 1/1000 trees. Four independent MCMC runs, each starting with random trees for each of four simultaneous chains, gave nearly the same results. Results were visualized using FigTree v. 1.4.3. Acronyms and

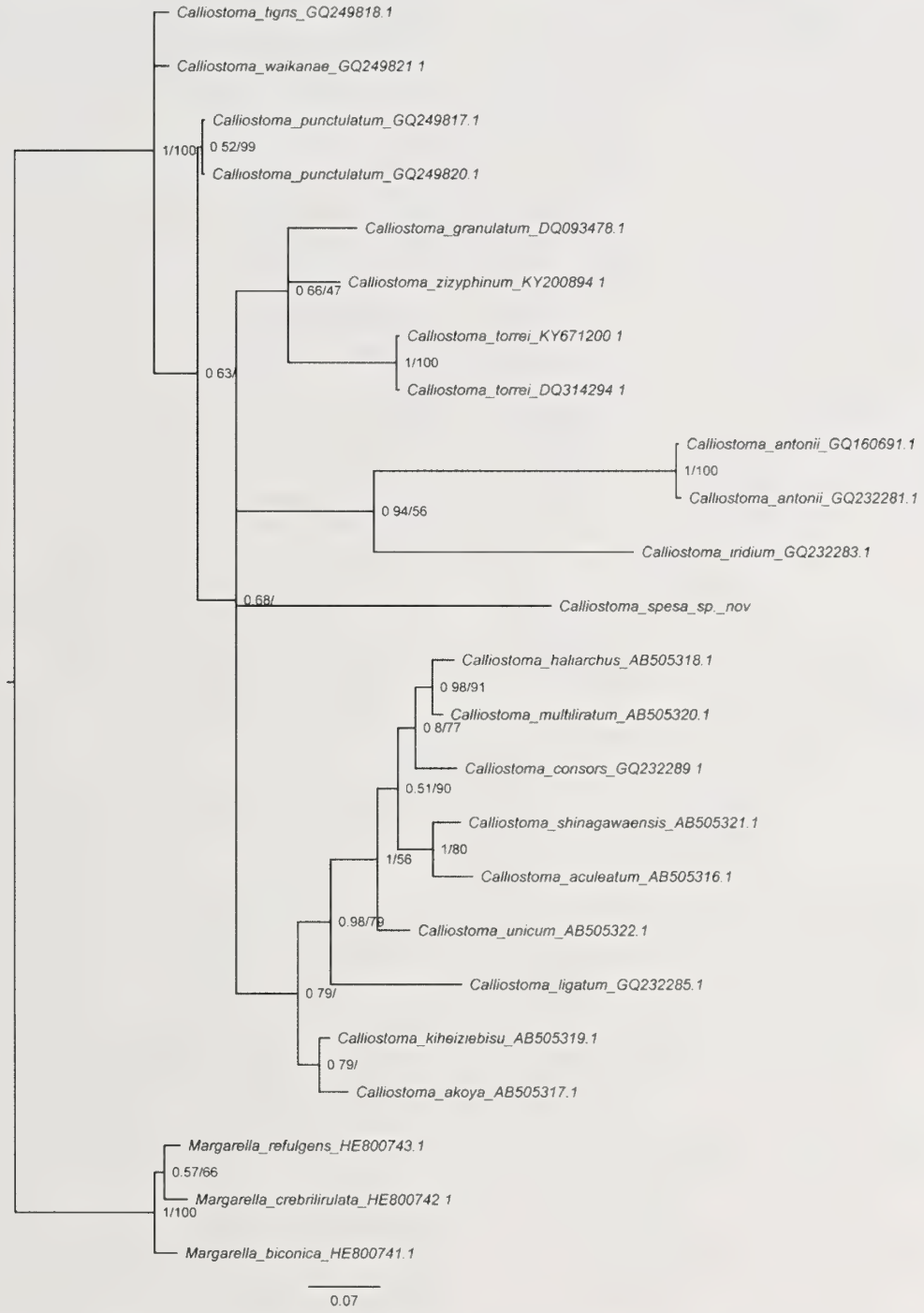

Figure 8. Phylogenetic tree inferred by Bayesian analysis (BI) and maximum likelihood (ML) from the mitochondrial 16S rRNA gene. Numbers adjacent to nodes refer to BI posterior probability (PP) and ML bootstrap scores (BS). Node value only show with BS > 50 and PP > 0.50.

abbreviations used throughout the text are: MBM: Marine Biological Museum, Chinese Academy of Sciences, Qingdao; XSM: Xiangri Shell Museum, Rizhao, China; P1, P2, P3,...: Primary cords (P1 is the most adapical); S1, S2, S3,...: Secondary cords (S1 is the most adapical).

SYSTEMATICS

Order Vetigastropoda Salvini-Plawen, 1980
Superfamily Trochoidea Rafinesque, 1815
Family Calliostomatidae Thiele, 1924 (1847)

Genus *Calliostoma* Swainson, 1840

Type Species: *Trochus conulus* Linnaeus, 1758 (by subsequent designation of Herrmannsen, 1846)

Calliostoma spesa new species
(Figures 1–7)

Description: Shell small, 8.8–10.1 mm in length, 7.7–8.5 mm in width, conical in shape, solid. Spire high, body whorl large. Protoconch of 1½ whorls, sculptured with network of threads that enclose hexagonal spaces.

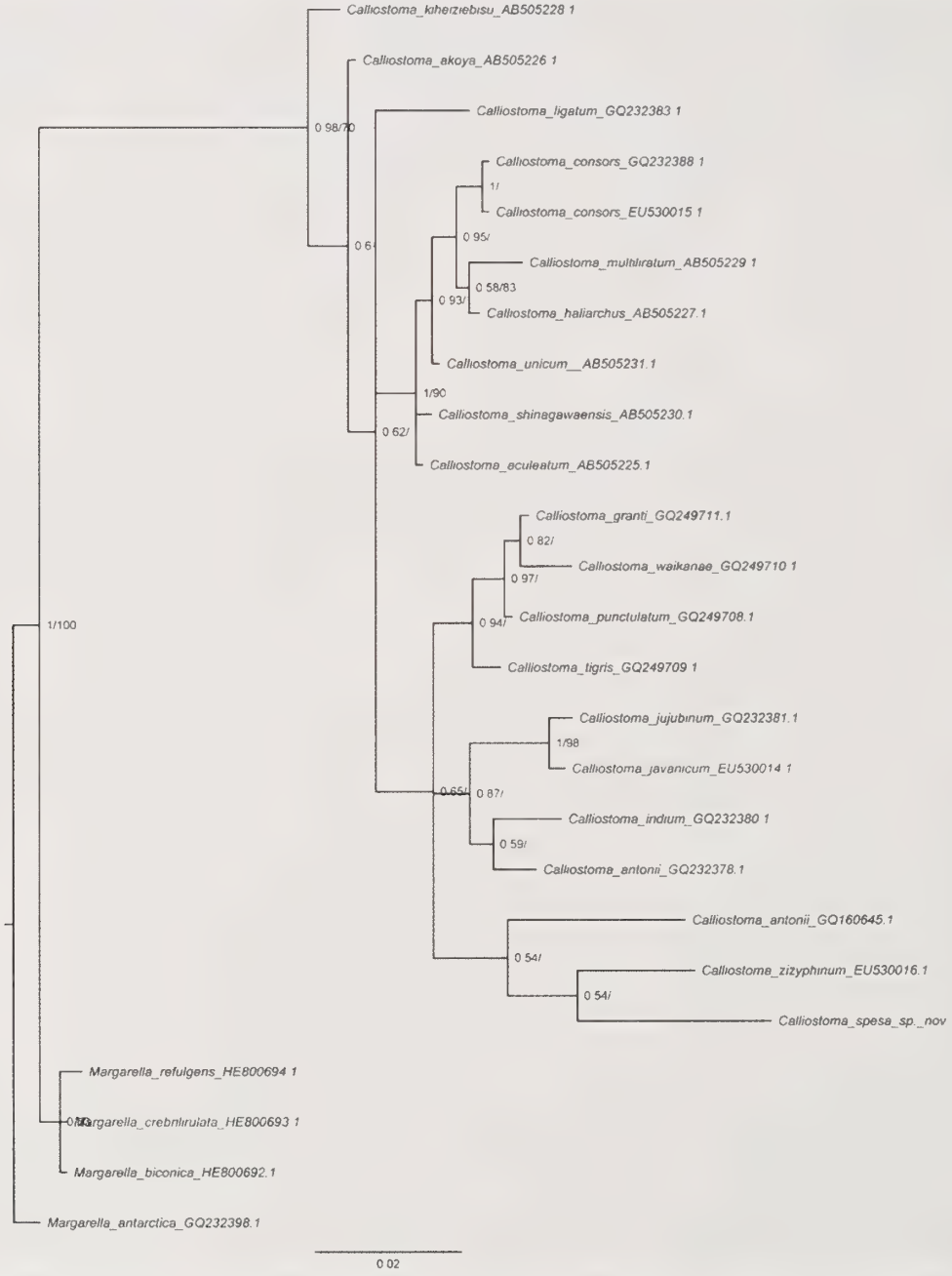

Figure 9. Phylogenetic tree inferred by Bayesian analysis (BI) and maximum likelihood (ML) from the nuclear 28S rRNA gene. Numbers adjacent to nodes refer to BI posterior probability (PP) and ML bootstrap scores (BS). Node value only show with BS > 50 and PP > 0.50.

Teleoconch of 8–9 whorls. Suture visible, thin, slightly constricted. First whorl weakly convex, almost flat; next whorls more convex, with a weak peripheral keel. Shell surface sculptured with dense spiral cords composed of strings of strongly beaded nodules. Interspace between the spiral cords thin and deep, irregularly spaced, smaller than cords. Each whorl with 5–6 spiral cords, including two stronger cords with thick beads at periphery. First teleoconch whorl with 3 cords, P2 and P3 appearing immediately, P1 appearing a quarter of whorl later; spiral cords with "granular" aspect caused by intersection with axial threads, aspect evenly spaced on entire whorl; P1 weaker than other cords; S3 completely hidden by succeeding whorl. On second whorl, P1 as strong as P2, P3 strongest; S3 appearing above suture. On third whorl, P3 strongest, S3 thickening, almost as strong as P1 and P2, but less strong than P3; S2 appearing at end of whorl, very thin. On fourth whorl, S3 thickening stronger than P1 and P2, but still less strong than P3; S2 thin and weak; beads on P1, P2 and P3 sharper than on S3. On next whorl, S3 strongest, forming keel; P1, P2 and S2 more or less similar in strength, with P3 stronger than them; beads of P1, P2, S2, and P3 triangular sharp; beads of S3 blunt; S1 appearing at end of whorl, very thin. On last whorl, S1 fully visible, granular but weaker than other cords; other spiral cords almost similar in size. Aperture broad, subquadrate; collumella curved, concave. Outer lip thin, with crenulated incision on margin. Inner lip slight thick, columellar lip smooth and nacreous. Anomphalous. Base flat, with about 9 weakly subgranular spiral cords of even thickness, interval between cords thin and deep. Shell purplish-red in color, spotted with irregular yellowish or brownish blotches. Color of beads on cords various covered by white and brown splotches or white and red splotches. Operculum corneous, yellowish, subcircular, multispiral, with subcentral nucleus.

Type Material: Holotype MBM229029 (length 10.1, width 8.5 mm), deposited in the MBM. Paratype (length 8.8 mm, width 7.7 mm), deposited at the XSM collection, unnumbered.

Type Locality: Weizhou Island, Guangxi Zhuang Autonomous Region, China, intertidal zone, coarse sandy bottom.

Distribution: Known only from the type locality.

Etymology: The specific epithet *spesa* was inspired by the Latin word *spes*, meaning hope. It is not used here as a formal derivation of that Latin word, but as a freely conceived name in apposition. The Type Material was collected by Chinese shell collector Mr. Xi Chen, whose nickname is "Hope".

Remarks: The new species is morphologically similar to *Calliostoma basulense* Poppe, Tagaro, and Vilvens, 2014, but the new species can be distinguished by the weak peripheral keel, strong beads at spiral cords, and deep thin interspaces between the spiral cords. *Calliostoma basulense* has flat, non-convex whorls, weaker nodules at spiral cords, and shallower interspaces.

Molecular Analyses: One sequence of the mitochondrial 16S rRNA and one of nuclear 28S rRNA genes were obtained from the new species. In the present study, we include available *Calliostoma* sequences from GenBank and species of subfamily Margarellinae Williams, 2013 as the outgroup. For each gene, the resulting two consensus trees established using BI and ML analyses were generally consistent; thus, a single topology was presented with support values indicated on branches (Figures 8 and 9). The phylogenetic trees show that *Calliostoma spesa* new species belongs in the *Calliostoma* clade but is genetically different from other species of *Calliostoma* obtained from GenBank. Species of genera *Calliostoma* and *Margarella* representing the subfamilies of Calliostomatinae and Margarellinae form two well-supported clades, respectively. Some species of *Calliostoma* used in present study, are assigned into different genera by WoRMS (see Table 1). But neither the 16S nor 28S phylogenetic trees support those allocations. Under current circumstances, the new species is placed within the genus *Calliostoma*. But, we cannot speak of its relationships with other species, in particular with those discovered from tropical Pacific, because most of the species were described mainly via shell morphology characters. There is a large number of species in this genus, but little information based on molecular data. The genetic information on this new species will hopefully help resolve phylogenetic relationships and generic allocations in the future.

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Rediscovery of *Cadulus podagrinus* Henderson, 1920: redescription, new records from the Bahamas, and discussions of its taxonomy (Scaphopoda: Gadilida: Gadilidae)

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ABSTRACT

Cadulus podagrinus Henderson, 1920 is reported from deep waters off the Bahamas, the first record since its original description. This new record of *C. podagrinus* extended the geographic distribution of the species northward by about 2,000 km. This species bathymetric distribution is also extended from 219 m to 465 m depth. The species is redescribed and the synonymy between *C. podagrinus* and its junior synonym *Cadulus halius* Henderson, 1920 is discussed.

Additional Keywords: shell morphology, morphometry, *Cadulus halius*

INTRODUCTION

Steiner and Kabat (2004) catalogued 517 extant and 816 extinct species of Scaphopoda, which is one of the smaller molluscan classes. The systematic and relationship of suprageneric groups of the class is relatively well known, with two orders recognized: Dentaliida and Gadilida (Reynolds and Steiner, 2008 and references cited therein).

Taxonomic revisions of the class were done for the Indo-Pacific fauna (Scarabino, 1995; Lamprell and Healy, 1998) and for the Atlantic Ocean fauna (e.g., Henderson 1920; Caetano et al., 2006, Scarabino and Caetano, 2008; Caetano et al. 2010; Scarabino and Scarabino, 2011). According to Scarabino and Scarabino (2011), about 130 species occur in the Atlantic Ocean, with 90 of them present in the western Atlantic. Henderson (1920) published the first comprehensive revision of scaphopods from the western Atlantic and, since then, the number of species in this area remained relatively stable (Scarabino and Scarabino, 2011).

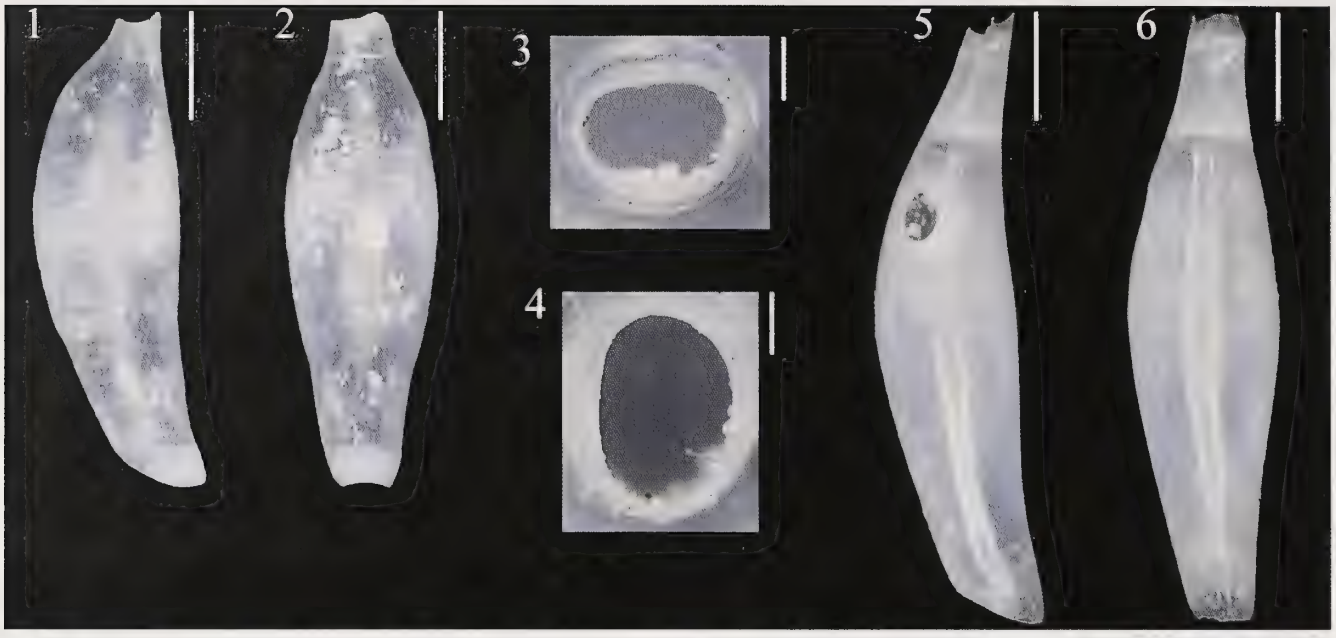
Henderson (1920) studied more than 70 species of Scaphopoda, of which 50 were described by him as new. Steiner and Kabat (2004: 555) stated that "This study led John B. Henderson to be one of the most prolific authors of Scaphopoda". About half of the species described by Henderson (1920) were classified in *Cadulus* Philippi, 1844. However, since Henderson's work the concept of *Cadulus* changed substantially, with numerous of his original sections or subgenera being elevated to genus status (see Palmer [1974] for details). Currently, the genus *Cadulus* has a worldwide distribution, with records since the Cretaceous, and occurring from the continental shelf to abyssal depths. The shell in this genus is characterized by having small to medium size (2–6 mm long), swollen appearance, maximum diameter in the center, a solid, smooth surface, color white when dead or translucent when fresh (Scarabino, 1995). The apertures are usually dorsoventrally or laterally compressed, the apex is simple or coronate, the preapical callus commonly prominent and the lumen is commonly circular (Scarabino 1995).

Cadulus podagrinus Henderson, 1920 was described based on three specimens, all of them collected from the type locality, off English Harbor, Antigua, 120 fathoms [equivalent to 219 m depth]. From the same sample, Henderson (1920) also described *Cadulus halius*. Steiner and Kabat (2004: 631–632) stated that *C. halius* Henderson, 1920 as a junior synonym of *C. podagrinus*, by first reviser action (ICZN 1999, article 24). According to the latter authors the holotypes of *C. podagrinus* and *C. halius* differ by the length between the dorsal aperture and the location of the maximum diameter, which could merely reflect the difference in the length of the specimens. *Cadulus podagrinus* is known only from its type locality.

Recently, examination of material deposited in malacological collections revealed new records of *C. podagrinus*, which represents a rediscovery of the species after almost a century. The shells identified provide new material to reassess the synonymy between *C. podagrinus* and *C. halius*.

MATERIALS AND METHODS

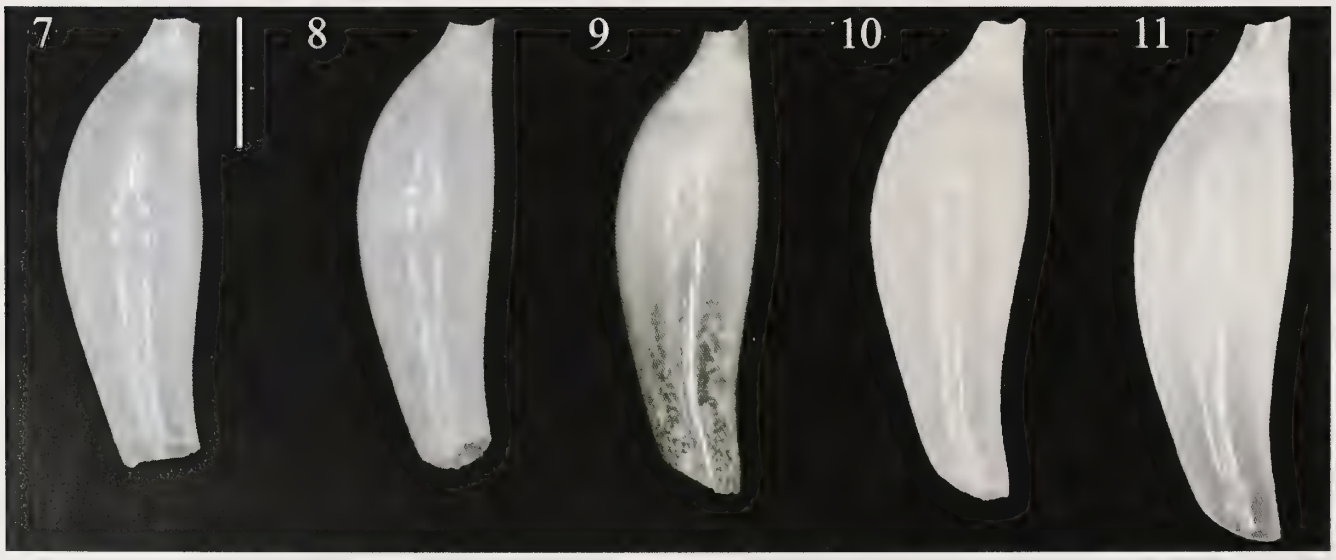
This report is based on specimens from the malacological collection of the Academy of Natural Sciences of Philadelphia, Drexel University (ANSP). Types of *C. podagrinus*



Figures 1–6. *Cadulus podagrinus* Henderson, 1920. **1–4.** *C. podagrinus*, **Holotype** USNM 596597. **5–6.** *Cadulus halius* Henderson, 1920, **Holotype** USNM 596599. **1, 5.** Shell in lateral view. **2, 6.** Shell in frontal view. **3.** Detail of posterior aperture. **4.** Detail of anterior aperture. Scale bars: 1–2, 5–6 = 1.0 mm; 3–4 = 200 μm.

Henderson, 1920 and *Cadulus halius* Henderson, 1920 housed at Smithsonian Institution's National Museum of Natural History (USNM) were also examined. The redescription of *C. podagrinus* is based on the amount of specimens identified. Descriptive terms of shell morphology are those of Scarabino (1995), who adopts a traditional view in that the apertures are the most anterior ("mouth" or anterior aperture) and posterior ("apex" or posterior aperture) regions. The material consist exclusively of empty shells and in the material examined number insided brackets indicate number of shells.

To aid the morphological study, morphometric variables were measured through photographs, following most of the variables used by Caetano et al. (2010). The following morphometric variables were used: shell length (L), maximum diameter (Max), distance of the point of maximum diameter from the anterior aperture (Dmax), height of anterior aperture (Ha), width of anterior aperture



Figures 7–11. Shells of *Cadulus podagrinus* Henderson, 1920 collected off the Bahamas, all in lateral view. **7–8, 10.** ANSP 368515. **9.** ANSP 368229. **11.** ANSP 369596. Scale bar: 1.0 mm, all specimens at same scale.

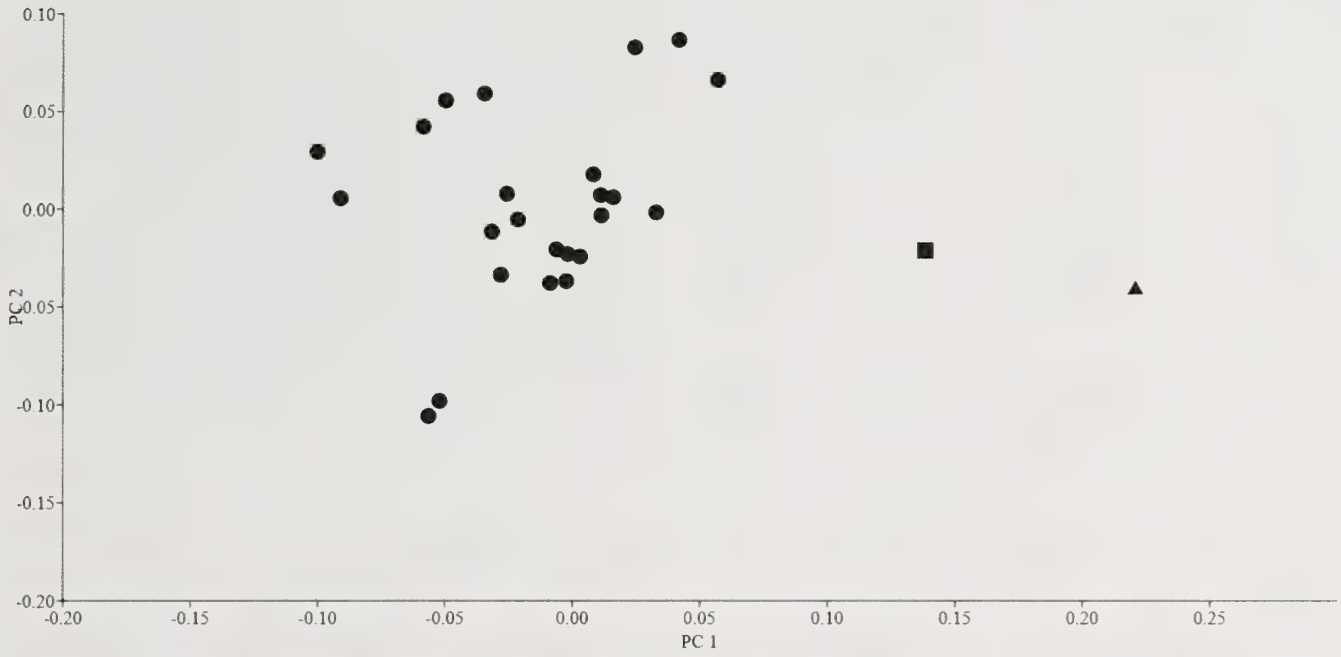


Figure 12. Principal Component Analysis of the shell morphometric data. Square= holotype of *Cadulus podagrinus* Henderson, 1920; Triangle= holotype of *Cadulus halius* Henderson, 1920; Dots= shells of *Cadulus podagrinus* from Bahamas.

(Wa), height of apex/posterior aperture (Hp), width of apex/posterior aperture (Wp). Variables related with curvature were not used because this species is only minimally curved.

The morphometric data was log transformed and a Principal Component Analysis (PCA) was performed using PAST3 (Hammer et al., 2001) to evaluate the variation of the morphometric variables.

SYSTEMATICS

Order Gadilida Starobogatov, 1974
Family Gadilidae Stoliczka, 1868

Genus *Cadulus* Philippi, 1844

Type Species: *Dentalium ovulum* Philippi, 1844, by monotypy. Recent, Mediterranean sea.

***Cadulus podagrinus* Henderson, 1920**
(Figures 1–11)

Cadulus (*Cadulus*) *podagrinus* Henderson, 1920: 148, pl. 20, fig. 5.
Cadulus (*Cadulus*) *halius* Henderson, 1920: 149, pl. 20, fig. 12.

Redescription: Shell up to 5.63 mm long, 1.38 mm wide, maximum diameter close to equator; translucent, glossy. In lateral view, ventral side is regularly curved until near the apex, region close to the apex is almost straight; dorsal side sinuous, alternating slightly concave and convex contours. In dorsal view, region close to anterior aperture has almost straight contour and is elongated; central region is convex, regularly curved; region close to posterior aperture almost straight in contour and elongated. Apex

Table 1. Measurements (in mm) of specimens examined in this study. SD = Standard Deviation; Min = minimum; Max = maximum. For abbreviation of morphometric variables, see Materials and Methods.

	C. podagrinus				*C. halius*
		ANSP, from Bahamas (n=24)			
	Holotype USNM 596597	Mean	SD (±)	Min–Max	Holotype USNM 596599
L	4.37	3.80	0.19	3.40–4.05	5.63
Max	1.35	1.22	0.07	1.06–1.38	1.31
Dmax	2.55	2.20	0.13	1.83–2.44	2.91
Ha	0.67	0.58	0.03	0.51–0.63	0.72
Wa	0.43	0.49	0.05	0.38–0.56	0.47
Hp	0.43	0.36	0.03	0.32–0.42	0.42
Wp	0.52	0.44	0.02	0.40–0.49	0.46

Table 2. Summary table of PCA analysis of the morphometric data of *Cadulus podagrinus*. PC= Principal Component.

PCs	Eigenvalues	% variance
1	0.00438314	50.71
2	0.00226973	26.259
3	0.000963595	11.148
4	0.000400395	4.6323
5	0.000365373	4.2271
6	0.000205637	2.3791
7	5,56E+00	0.64368

wide, oval, compressed dorsoventrally, bilobed, one lobe in ventral side and other in dorsal side. Preapical callus thin, lumen dorsoventrally oval. Anterior aperture wide, oval, laterally compressed, oblique in lateral view.

Type Locality: Off English Harbor, Antigua, 120 fathoms [equivalent to 219 m depth], State University of Iowa Expedition, sta. 115, 1918.

Type Material: Holotype: USNM 596597; **Paratypes:** USNM 596598 [1], USNM 314935 [2], both from type locality. *Cadulus halius*: **Holotype:** USNM 596599, off English Harbor, Antigua, 219 m depth, State University of Iowa Expedition sta. 115, 1918; paratypes: USNM 314936 [5], from type locality (same type locality as *Cadulus podagrinus*).

Material Examined: Holotype of *C. podagrinus*; Holotype of *C. halius*. Bahamas (all originally as *Cadulus* sp.): Memory Rock, Grand Bahama Island (26°57′ N, 79°06′ W, 464 m depth), coll. Rose, B.: ANSP 368229 [4]; Wood Cay, Grand Bahama Island (26°44′15″N 79°58′15″W, 465 m depth), coll. Rose, B.: ANSP 369596 [15]; West End, Grand Bahama Island (26°42′15″N 78°59′50″W, 305 m depth), coll. Rose, B.: ANSP 368515 [5].

Measurements: see Table 1 and Appendix 1.

Distribution: Bahamas (this study); Antigua and Barbuda (Henderson 1920). Empty shells occuring from 219 m (Henderson 1920) to 465 m depth (this study).

Remarks: The shells from Bahamas identified here match the morphology of the holotype of *C. podagrinus* (Figures 1–4), showing an inflated shell, very convex in the central region, and with the region close to dorsal aperture shorter and straight (Figures 7–11). The holotype of *C. halius* (Figures 5–6) has the region close to dorsal aperture more elongated than the holotype of *C. podagrinus* (Figures 1–2) and than the Bahamian specimens (Figures 7–11). We have not found any intermediate stage of growth between the types of *C. podagrinus* and *C. halius*.

Despite the difference of more than 1.0 mm in shell length between the types of *C. podagrinus* and *C. halius* (Table 1), the maximum diameter (Max) and dimensions of apertures (Ha, Wa, Hp, Wp) present smaller differences in these shells (Table 1). In Scaphopoda, during growth the mantle margin secretes the shell in both apertures. In the posterior aperture, shell absorption occurrs to keep the aperture open for metabolic activities (e.g., water circulation, gas exchange) (Palmer and Steiner, 1998). Thus, during growth the posterior aperture can remain with a similar dimension, which can explain these small differences of Hp and Wp.

The component 1 and component 2 of the PCA explain 50.7% and 26.3%, respectively, of the variation of the sample, that is 77% of the variation (Table 2). At the component 1, the variables L and Dmax explain most of the variation (Table 3). The holotypes of *C. podagrinus* and *C. halius* show the highest scores in the component 1, more distant from the remaining shells. This can be explained by the size-effect, as both show the highest values of L and Dmax, the remaining shells are younger specimens.

Despite these assumptions, we remain skeptical about the proposed synonymy between *C. podagrinus* and *C. halius*. A greater number of specimens of similar size to the holotype of *C. halius* would be useful to investigate the late ontogeny of the species and reassess the synonymy of these names.

The most similar species in the Atlantic is *Cadulus nerta* Caetano, Scarabino and Absalão, 2006, however, as noted by Caetano et al. (2006) "it is less inflated, smaller and has a more laterally compressed apertural section".

The new record of *C. podagrinus* in Bahamas (±26°N) represent a rediscovery of the species after almost a century (Henderson 1920) and extends northward the geographic distribution of the species. *Cadulus podagrinus* was known only from the type locality (±17°N). The bathymetric distribution is also extended from 219 m to 465 m depth. The species is known only by empty shells.

Table 3. Component loadings for each morphometric variable of *Cadulus podagrinus*.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
L	0.58336	-0.12312	0.24622	-0.24915	-0.24491	0.26841	-0.62434
Max	0.30608	0.23067	0.031113	0.4668	0.54188	-0.4688	-0.34761
Dmax	0.50882	-0.18827	0.26826	-0.40903	0.19302	-0.34136	0.55911
Ha	0.32915	-0.24857	0.1539	0.73059	-0.21471	0.32336	0.34895
Wa	-0.013899	0.80716	0.53351	-0.010881	-0.12281	0.15423	0.15707
Hp	0.37359	0.37475	-0.6283	0.0086704	-0.49668	-0.25863	0.10757
Wp	0.2429	0.20603	-0.40418	-0.13697	0.54886	0.62962	0.13697

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Appendix 1. Raw data of shell morphometric variables of *Cadulus podagrinus* Henderson, 1920.

Lot	L	Max	Dmax	Ha	Wa	Hp	Wp
Holotype of *C. podagrinus* USNM 596597	4.37	1.35	2.55	0.67	0.43	0.43	0.52
Holotype of *C. halius* USNM 596599	5.63	1.31	2.91	0.72	0.47	0.42	0.46
ANSP 368229	3.96	1.16	2.35	0.58	0.48	0.35	0.42
ANSP 368229	3.56	1.18	2.11	0.56	0.55	0.34	0.43
ANSP 368229	3.73	1.20	2.05	0.56	0.55	0.36	0.46
ANSP 368229	3.67	1.11	2.21	0.61	0.41	0.32	0.40
ANSP 368515	3.70	1.21	2.17	0.59	0.45	0.34	0.44
ANSP 368515	3.72	1.19	2.09	0.60	0.47	0.37	0.44
ANSP 368515	3.84	1.16	2.20	0.57	0.49	0.34	0.42
ANSP 368515	3.40	1.19	1.83	0.58	0.52	0.34	0.41
ANSP 368515	3.48	1.06	2.09	0.51	0.49	0.35	0.42
ANSP 369596	3.80	1.25	2.28	0.59	0.47	0.34	0.44
ANSP 369596	3.97	1.22	2.30	0.57	0.46	0.32	0.45
ANSP 369596	3.99	1.19	2.31	0.56	0.45	0.34	0.45
ANSP 369596	3.77	1.34	2.25	0.59	0.47	0.38	0.44
ANSP 369596	3.91	1.32	2.32	0.60	0.51	0.35	0.41
ANSP 369596	3.67	1.10	2.10	0.59	0.38	0.34	0.41
ANSP 369596	4.05	1.28	2.32	0.63	0.50	0.35	0.45
ANSP 369596	3.52	1.19	1.99	0.52	0.50	0.40	0.46
ANSP 369596	3.77	1.20	2.19	0.60	0.52	0.33	0.44
ANSP 369596	4.03	1.25	2.34	0.58	0.50	0.33	0.46
ANSP 369596	3.78	1.22	2.21	0.57	0.43	0.37	0.49
ANSP 369596	3.90	1.27	2.14	0.59	0.56	0.41	0.47
ANSP 369596	3.86	1.26	2.17	0.59	0.49	0.37	0.47
ANSP 369596	4.02	1.29	2.28	0.54	0.55	0.42	0.48
ANSP 369596	4.02	1.38	2.44	0.57	0.55	0.39	0.46

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